Proceedings of the 9th ICAZ Conference, Durham 2002

# Recent Advances in Ageing and Sexing Animal Bones

Edited by Deborah Ruscillo

Oxbow Books

# Recent Advances in Ageing and Sexing Animal Bones

*For Vasili and Marilena*

*Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August 2002*

Series Editors: Umberto Albarella, Keith Dobney and Peter Rowley-Conwy

# Recent Advances in Ageing and Sexing Animal Bones

Edited by
Deborah Ruscillo

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*Published by*
Oxbow Books, Park End Place, Oxford OX1 1HN

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ISBN 978 1 842 17122 6 1 84217 122 4

A CIP record for this book is available from The British Library

*This book is available direct from*
Oxbow Books, Park End Place, Oxford OX1 1HN
(Phone: 01865–241249; Fax: 01865–794449)

*and*

The David Brown Book Company
PO Box 511, Oakville, CT 06779, USA
(Phone: 860–945–9329; Fax: 860–945–9468)

*and*

via our website
www.oxbowbooks.com

*Cover image: Ursus americanus baculum, mandible and innominate, photo taken by Haskel Greenfield*

Printed in Great Britain at
Antony Rowe, Chippenham

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# Preface

*Umberto Albarella, Keith Dobney and Peter Rowley-Conwy*

This book is one of several volumes which form the published proceedings of the 9th meeting of the International Council of Archaeozoology (ICAZ), which was held in Durham (UK) 23rd–28th August 2002. ICAZ was founded in the early '70s and has ever since acted as the main international organisation for the study of animal remains from archaeological sites. The main international conferences are held every four years, and the Durham meeting – the largest ever – follows those in Hungary, the Netherlands, Poland, England (London), France, USA, Germany and Canada. The next meeting will be held in Mexico in 2006. The Durham conference – which was attended by about 500 delegates from 46 countries – was organised in 23 thematic sessions, which attracted, in addition to zooarchaeologists, scholars from related disciplines such as palaeoanthropology, archaeobotany, bone chemistry, genetics, mainstream archaeology etc.

The publication structure reflects that of the conference, each volume dealing with a different topic, be it methodological, ecological, palaeoeconomic, sociological, historical or anthropological (or a combination of these). This organisation by theme rather than by chronology or region, was chosen for two main reasons. The first is that we wanted to take the opportunity presented by such a large gathering of researchers from across the world to encourage international communication, and we thought that this could more easily be achieved through themes with world-wide relevance. The second is that we thought that, by tackling broad questions, zooarchaeologists would be more inclined to take a holistic approach and integrate their information with other sources of evidence. This also had the potential of attracting other specialists who shared an interest in that particular topic. We believe that our choice turned out to be correct for the conference, and helped substantially towards its success. For the publication there is the added benefit of having a series of volumes that will be of interest far beyond the restricted circle of specialists on faunal remains. Readers from many different backgrounds, ranging from history to zoology, will certainly be interested in many of the 14 volumes that will be published.

Due to the large number of sessions it would have been impractical to publish each as a separate volume, so some that had a common theme have been combined. Far from losing their main thematic focus, these volumes have the potential to attract a particularly wide and diverse readership. Because of these combinations (and because two other sessions will be published outside this series) it was therefore possible to reduce the original 24 sessions to 14 volumes. Publication of such a series is a remarkable undertaking, and we are very grateful to David Brown and Oxbow Books for agreeing to produce the volumes.

We would also like to take this opportunity to thank the University of Durham and the ICAZ Executive Committee for their support during the preparation of the conference, and all session organisers – now book editors – for all their hard work. Some of the conference administrative costs were covered by a generous grant provided by the British Academy. Further financial help came from the following sources: English Heritage, Rijksdienst voor het Oudheidkundig Bodemonderzoek (ROB), County Durham Development Office, University College Durham, Palaeoecology Research Services, Northern Archaeological Associates, Archaeological Services University of Durham (ASUD), and NYS Corporate Travel. Finally we are extremely grateful for the continued support of the Wellcome Trust and Arts and Humanities Research Board (AHRB) who, through their provision of Research Fellowships for Keith Dobney and Umberto Albarella, enabled us to undertake such a challenge.

The present volume publishes the proceedings of the session 'Ageing and Sexing', which was among the first to be proposed for ICAZ 2002 and ended up being one of the strongest and best attended. This was in large part due to Deborah Ruscillo's excellent organisational skills, but also to the inherent interest and appropriateness of this subject for an ICAZ conference. Whether we study material from Argentina or Japan, from the Palaeolithic or the medieval

period, we still need to deal with the issue of ageing and sexing animal bones. A methodological session may be of little interest outside the field of zooarchaeology, but this is compensated for by the fact that *all* animal bone specialists will be interested in it. Initially Deborah wanted simply to find the best venue to present her interesting new method of sexing mammal bones through shape analysis. However, here was an opportunity to be more ambitious and organise a whole session dedicated to sexing and ageing studies. Things went ahead as planned and this book represents the culmination of almost three years of work, begun with a cosy conversation in the warm environment of the Ruscillo/Cosmopoulos home in Winnipeg (as the external temperature approached *minus* 30°C!).

The publication in 1982 of the volume "Ageing and sexing animal bones from archaeological sites", edited by Bob Wilson, Caroline Grigson and Sebastian Payne, represented a milestone in the development of zooarchaeological studies, and the book is, unsurprisingly, one of the most cited publications in zooarchaeology. Since then, as Terry O'Connor highlights in his introduction to the present volume, much more work has been done in refining ageing and sexing methods and in improving our understanding of body development and sexual variation in the vertebrate skeleton. However, so far zooarchaeologists are still by and large adopting ageing and sexing methods that are pre- rather than post- 1982. The challenge of this book is therefore not just to add more information, but also to persuade zooarchaeologists that the time is ripe for experimenting with new methods and for analysing data by taking into account the substantial new advances that this discipline has produced in more recent years. Only time will tell if this volume will have achieved this ambitious goal, but whatever the case, we have little doubt that it will represent an indispensable tool for zooarchaeologists worldwide.

Final special thanks must go to Vasili and Marilena Cosmopoulos (Deborah's son and daughter), who had the good grace to be born during the final stages of the editing of this volume. We could not have expected a better omen for the success of the book.

# Acknowledgments

These proceedings are a direct result of the teamwork and collegiality of the authors involved. Always polite and accommodating, the participants of the Ageing and Sexing Session were a pleasure to work with, and I thank them for their cooperation and their contributions to methodology in zooarchaeology. The participants of the session also acted as referees of the published proceedings; each participant reviewed two papers submitted for publication to ensure the quality and accuracy of the information presented herein. For the sake of keeping costs low, raw data for the various studies presented in this volume could not be published. The authors are happy to provide raw data from their research upon request (addresses provided at the end of each chapter).

The session would not have been such a success were it not for the tireless support and direction of the conference organizers. This publication was made possible by these same individuals who also bravely took on the series editing and organization after the conference ended. On behalf of all the participants of the Ageing and Sexing Session, I wish to express our appreciation for the commitment of Umberto Albarella, Keith Dobney, Peter Rowley-Conwy and Deborah Jaques for the conference preparations and publication series organization. I would also like to thank Simon Davis and Caroline Grigson for chairing the morning and afternoon sections of the ageing and sexing colloquium, and also for acting as referees for some papers submitted here.

Travel and accommodation grants for the participants were supplied thanks to generous funding from the Institute for Aegean Prehistory (INSTAP). We are grateful for their support and their broad vision of archaeological research. INSTAP is one of the few organizations that realize the potential of zooarchaeological studies in the quest of studying ancient peoples.

*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 1–8*

# 1. Vertebrate Demography by Numbers: Age, Sex, and Zooarchaeological Practice

*T. P. O'Connor*

*An overview of technical developments in the attribution of age and sex to ancient bones shows that considerable advances have been made in some techniques, such as in the resolution of age at death from dental evidence, and much less in others, notably the analysis of epiphysial fusion. The quality of modern analogue data remains a problem, and one that is not helped by the husbandry practices current throughout much of the world. Limits to the resolution of the zooarchaeological data are set in part by the limitations of our techniques, and in part by the underlying biological processes. Understanding those processes, and therefore the limits beyond which technical developments cannot take us, is a priority. Attribution to sex remains an urgent issue in all analyses of hunting and husbandry, but one that has made only limited advances in recent years. The use of multivariate shape analysis offers the prospect of improving our simple interpretations of uni- or bivariate metrical analyses. Ancient DNA analysis offers a new approach to the attribution of sex, but is likely only to be applicable to limited numbers of specimens in particular circumstances. Perhaps the most pressing area for further research and development lies in the inference of information from our demographic data, both in understanding the taphonomy of the assemblages and hence the population that they represent, and in developing mortality models as an heuristic device to aid data interpretation.*

Although zooarchaeology uses Linnaean taxonomy, it is a valid assumption that the people who lived and worked with domestic and wild animals in the past, just as today, used a much more subtle taxonomy, subdividing what we would recognise as species by sex, calendar age, state of growth, and many more parameters. Zooarchaeologists acknowledge that more precise taxonomy by seeking to recognise amongst archaeological bones the traits that enable us to classify them by developmental or calendar age, and, less often, by sex. Other contributions to this volume show the state of research in particular techniques, or the success with which age and sex estimation methods have been applied in particular case studies. This introductory paper reviews the last couple of decades, to assess how successful zooarchaeology has been in the analysis of demography and mortality, and to consider what the challenges might be for the foreseeable future. Twenty years is a convenient length of retrospect because it is that long since the publication of a very influential compilation of papers on this subject (Wilson *et al.* 1982), and ends conveniently with another (Pike Tay 2002).

## Age

To start with age at death estimation, the most widely-applied techniques to date have been based on dental eruption and attrition, on crown-height measurement (itself an integration of eruption and attrition), and on epiphysial fusion. Teeth remain the age-estimation data source of choice in most projects. The sequence and timing of the eruption of deciduous and permanent teeth provides a developmental scale of surprising stability, apparently remaining relatively unaffected by the growing environment of the individual animal (e.g. see Franklin 1950).

The challenge that has beset analyses of tooth eruption is the quality, or otherwise, of the modern analogue data. The eruption data given in earlier sources, such as the much-quoted Silver (1969), were often derived from veterinary or agricultural sources, not from direct observation of accurately known-age specimens. We could probably agree that a tooth begins the process of eruption when the crown begins to emerge from the crypt, and completes that process when the crown of the tooth fully reaches the occlusal plane and begins to acquire some attrition of the enamel, two stages picked out in the recording procedures developed by Payne (1973) and Grant (1982). A farmer or veterinarian, however, might describe eruption as occurring when the tooth breaks through the gum, which is neither of those stages. That discrepancy imposes a degree of uncertainty on the eruption dates that we can acquire from the literature, and even on the sequence of eruption. Payne (1984) noted that 19th century sources seem to show cattle LM3 and P4 erupting in a different order to that commonly observed in ancient material. Does that indicate something significant about microevolution in domestic cattle, or about the differing definitions of 'erupting'? Correlating the veterinary and agricultural literature with zooarchaeological observations continues to be problematic, even for the most familiar and well-studied of domestic ruminants.

It is for just that reason that direct studies of known-age material have been undertaken. Wilson *et al.* (1982) included some of these, and subsequent examples have included a review of dental data for sheep by Moran and O'Connor (1994). That survey was of sheep from many different populations, held in a number of collections. The general consistency that was noted is encouraging, though a clear discrepancy in the time of eruption of LM3 was noted between a cohort of Soay sheep and the remainder of the sample. It can be reassuring to be able to compare studies of a genetically mixed sample with a much more homogeneous cohort. For pigs, for example, we have a very good population study by Bull and Payne (1982), and it would be useful to have a comparandum drawn from a much wider series of pig populations. Apart from veterinarians and farmers, wildlife managers need to be able to estimate age at death, and the wildlife management literature includes a great many papers on dental development in diverse species. Fig.1 summarises at least some of these sources, not as a comprehensive list but as an illustration of the diverse taxa for which at least some data exist.

| **Species** | **Reference(s)** |
|---|---|
| *Castor fiber* | Hatting 1969 |
| *Ondatra zibethicus* | Doude van Troostwijk 1976 |
| *Marmota monax* | Munson 1984 |
| *Spermophilus beecheyi* | Adams and Watkins 1967 |
| *Meles meles* | Ahnlund 1976 |
| *Felis catus* | Berman 1974 |
| *Canis latrans* | Roberts 1978 |
| *Sus scrofa* | Bull and Payne 1982; Weaver *et al.* 1969; Matschke 1967 |
| *Pecari tajacu* | Kirkpatrick and Sowls 1962 |
| *Hippopotamus amphibius* | Laws 1968 |
| *Capreolus capreolus* | Aitken 1975; Carter 1997 |
| *Dama dama* | Brown and Chapman 1990; Moore *et al.* 1995 |
| *Cervus elaphus* | Brown and Chapman 1991; Kierdorf and Becher 1997; Klein *et al.* 1981; Lowe 1967; Mitchell 1967; Quéré and Pascal 1983; Keiss 1969 |
| *Rangifer tarandus* | Hufthammer 1995; Miller 1972; Sokolov *et al.* 1996 |
| *Odocoileus hemionus* | Robinette *et al.* 1957; Main and Owens 1995 |
| *Hemitragus jemlahicus* | Caughley 1965 |
| *Bison* sp. | Frison and Reher 1970; Novakowski 1965 |
| *Bos* sp. | Andrews 1973; Wiener and Forster 1982; Andrews and Wedderburn 1973; Brown *et al.* 1960 |
| *Ovis* spp. | Hemming 1969; Moran and O'Connor 1994 |
| *Capra hircus* | Noddle 1974; Deniz and Payne 1982 |
| *Gazella* spp. | Davis 1980 |

*Fig. 1. Sources for age at death estimation based on studies of dentition in modern populations. The list is by no means exhaustive. It is intended to show the range of data available in the literature, and the particular preoccupation with certain taxa.*

A welcome development in recent years has been the detailed study of root development as a measure of eruption stages. Carter (1997; 1998; Chapter 3 in this volume), in particular, has shown that x-radiographic imaging of ruminant mandibles allows stages of eruption to be defined with considerable precision, and has used that procedure to undertake a re-analysis of seasonality of occupation at northern European Mesolithic sites. The procedure is non-destructive and technically simple, only requiring the production of good-quality x-radiographs, though that may require more technical skill than is sometimes allowed.

Once the adult dentition is fully erupted by whatever definition, age estimation becomes notoriously difficult, as we resort to recording the state of attrition of the teeth. Probably the most frequently cited paper in Wilson *et al.* (1982) is Annie Grant's protocol for recording dental attrition in cattle, sheep, and pigs, based on changes in the pattern of dentine exposure across the occlusal surface of 4th premolar and molars. Sebastian Payne's similar recording system for caprines (1973; 1987) probably gives greater resolution for that taxon, though the greater convenience of being able to record all three of the main Old World domesticates on the same system has led to Grant's recording protocol being widely used. Something of the difficulty of recording attrition data consistently was shown by Gibson (1993) with his development of an automated expert system for recording and analysing dental eruption and attrition data in, inevitably, sheep. To build the system required a step-by-step analysis and emulation of the whole process of viewing and recording an occlusal surface, and showed how complex and potentially subjective that apparently simple procedure can be. As part of his study, Gibson undertook a 'blind' test in which zooarchaeologists recorded a number of sheep mandibles as a test of inter-observer consistency. The results were not altogether reassuring, though we might take comfort from the observation that the more experienced participants showed the greatest consistency.

The other approach to attrition has been the measurement of crown height, a well-established procedure, and one that lends itself well to age-estimation in taxa in which attrition proceeds rapidly, hence Davis' (1983) successful application to *Gazella,* Levine's (1982) to *Equus*, and Steele's (Chapter 7 in this volume) to *Cervus*. However attrition is recorded, our confidence in the data depends upon an assumption that the rate of attrition in that species does not vary considerably between populations, otherwise we cannot use modern data to calibrate our archaeological results and cannot directly compare different archaeological samples. For at least some taxa, there are modern data that quantify the inter-population variation in attrition rates. It is, perhaps, no surprise that much of the evidence relating to sheep comes from New Zealand (Barnicoat 1963; Healy and Ludwig 1965; Cutress and Healy 1965; Ludwig *et al.* 1966; Healy *et al.* 1967). These studies show the importance of soil ingestion, and thus of grazing quality (and perhaps, grazing density) in affecting the rate of dental attrition. In other words, there might be an additional feedback mechanism between husbandry and one of the key parameters that we use to investigate husbandry-related mortality. Something similar has been shown in free-living reindeer populations (Sokolov *et al.* 1996). Variation in attrition rates is an issue that might not be confined to domestic mammals. Comparisons of wear rate and durability between grazing and browsing ruminants appear to show a consistent relationship between the durability of different molars and the feeding habit (Solounias *et al.* 1994; Steele, Chapter 7 in this volume).

Can we see a similar degree of inter-population variation in archaeological material? It has been possible to show that medieval samples of sheep mandibles from sites in York show measurable differences in the attrition rate of the permanent molars (Bond and O'Connor 1999, 387–391). More studies of this nature would enable us to see whether variation in attrition rates has been widespread and large enough in magnitude to be a general problem that we need to tackle, or one particular to certain places and some periods of time. At the moment, we may have a strong suspicion, but lack enough evidence to do more than some inductive speculation from a few case studies.

Another age at death procedure that was touched on by Wilson *et al.* was the analysis of incremental structures in dental cementum. This is a field of investigation that was already well-established in wildlife management (e.g. Adams and Watkins 1967; Aitken 1975). Saxon and Higham (1968) gave a particularly perceptive demonstration of its application to zooarchaeology; the procedure has shown real advances in the intervening years. In particular, it is significant that the formation of cementum increments has been investigated from the underlying biology upwards, thus validating the empirical associations that are made between cementum counts and age in known-age modern data (Lieberman 1994). What this has shown is that the correlation between increments and calendar years is not an exact one (Keay 1996), but at least the modern studies have indicated the extent and likely causes of the discrepancies that can arise. As with so much in zooarchaeology, there have been calls for a standardisation of terminology (Gordon 1993). The use of image-analysis methods to facilitate the analysis of increment data is to be welcomed (Lieberman *et al.* 1990; Lieberman and Meadow 1992). The gadget might not be any more accurate than a skilled human observer, but at least its subjectivity is likely to be constant from one sample to the next. One of the major applications of increment analysis, of course, has been in the investigation of seasonality (e.g. see Burke and Castanet 1995; Martin 1998). Although that is not the main topic of this session, our ability to investigate seasonal husbandry and hunting is inextricably bound up with our

ability to resolve age at death both precisely and confidently (O'Connor 1998).

The maturation of the post-cranial skeleton, in particular fusion of the appendicular epiphyses, constitutes the other major approach of age estimation. It would be unfair to say that there has been *no* significant advance since 1982. However, it does seem that research has been inhibited by the problems inherent in constructing a sample mortality profile from epiphysial fusion data, relating the zooarchaeological data to modern data full of inconsistencies and uncertainties. Perhaps this is not surprising: when Moran and O'Connor (1994) reviewed published sources on epiphysial fusion in the sheep, they found serious discrepancies in the fusion times given by different researchers. Some of those discrepancies have probably arisen because studies such as Smith (1956) identified epiphysial fusion by radiography of live animals, whilst others have investigated macerated bone specimens. Investigation of epiphysial fusion by radiography requires the confident recognition of specific tissues from their x-ray image, and poses the additional challenge of interpreting a 2-dimensional radiograph in terms of growth events on an irregular anatomical surface positioned at right-angles to the film plane. From a careful reading of the radiographic criteria that Smith used, it is likely that he was recording as 'fused' specimens at an earlier stage of maturation of the epiphysial plate, in which bony fusion had not yet occurred. A less problematic application of radiography to age estimation was Dhingra's (1976) use of x-rays to determine the age at which ossification of the metatarsal sesamoid begins in four bovid species.

Apart from discrepancies in the modern data, epiphysial fusion has been shown to be affected by factors such as nutritional plane and castration. Moran and O'Connor detected a delay in epiphysial fusion in castrated sheep in their study, but only in the 'intermediate' fusing epiphyses; not in the earliest or latest fusing ones. Perhaps castration has more effect on the trajectory of skeletal maturation than on the final outcome: there are some hints to that effect, too, in Tchirvinsky's (1909) early study of the subject. Davis (2000) noted delay of epiphysial fusion in castrates when compared with intact males in a well-controlled sample of Shetland sheep. Epiphysial fusion data remain problematic, a useful source of information on those rare occasions that we have an articulated individual skeleton to study, but difficult and uncertain when we have only disarticulated elements from, at best, an approximately estimated number of individuals. That said, some projects have made good use of epiphysial fusion data, not least Zeder's (2001; Chapter 6 in this volume) ingenious integration of biometric and epiphysial data in her investigation of *Capra* mortality at a group of sites in Iran and Iraq.

Among the age-estimation methods that did not appear in Wilson *et al.* was the analysis of osteons, whether as counts per unit area, or as estimates of the proportion of cortical bone re-organised into secondary osteons. This is a source of information that has been explored most thoroughly for the human skeleton (Kerley 1965; Stout and Stanley 1991; Aiello and Molleson 1993), though some correlation with age has been shown in other species. Dammers (Chapter 2 in this volume) shows that osteons can be quite useful in zooarchaeological studies. In *Capreolus*, more specifically, Jane Ruddle (1996) was able to show a sufficiently close association between secondary osteon development and calendar age to give hope that this technique will develop in the coming years. Like the analysis of cementum increments, it requires destructive sampling. We zooarchaeologists might think it worthwhile to undertake a little destruction in return for useful data, but those who curate the collections that we study might think otherwise. The more destructive techniques therefore have to be particularly well founded and convincing.

## Sex

Identification of the sex of vertebrates occupied the smaller part of Wilson *et al.*, perhaps reflecting a view in the early 1980s that age-estimation offered more opportunity for significant advances to be made. Discontinuous sex-specific traits, such as the distinctive morphology of the canine teeth in male suids, or the possession of antlers in male cervids, or the presence of a baculum in males of some taxa, offer a simple means of recognising that a sample of bones includes both males and females of a particular species. Quantification can be more problematic. If a sample contains a minimum of six wolves, but only two bacula, we can not say that the other four individuals were female. Antlers are limited in their value, because they are shed annually, and collected as raw material for artefacts. The presence of antlers in a sample of *Cervus* bones, for example, allows no confident attribution of sex to the post-cranial bones in the same sample. With suid canines, we can at least link age and sex in our analysis of a sample of mandibles. With individual skeletons, the ability to attribute sex can be more directly useful, showing, for example, that the great majority of Migration Period and Merovingian horse burials from northern Europe are males (O'Connor 1994).

The presence of medullary bone in birds is a simple indicator of sex, albeit one that is cyclically present and absent. Driver's paper in Wilson *et al.* showed that an analysis of medullary bone can be used to investigate the demography of domestic fowl bones. The possibility of using medullary bone as an indicator of seasonal foraging has been mentioned by some authors (e.g. Monks 1981), but the subject has received comparatively little attention. A notable exception is Lentacker and Van Neer's (1996) detailed study of the occurrence of medullary bone in domestic fowl from Roman deposits at Berenike, Egypt.

The authors use the comparatively high frequency of occurrence of medullary bone to argue that most of the Berenike specimens represent females killed during the breeding season. However, they also suggest that medullary bone is under-recorded, noting an increase in their own recognition of medullary bone in assemblages recorded after Berenike.

Much of our investigation of sex in ancient vertebrates is based on continuous data, and on deciding whether biometric bimodality denotes sexual dimorphism. Sometimes, the degree of dimorphism is large enough barely to need measuring – the depth of the acetabular margin in domestic bovids, for example (see Greenfield, Chapter 5 in this volume). Too often, though, we are reduced to the statistical investigation of size distributions, to detect significant bimodality, and then to deciding whether that bimodality is most likely to be sexual dimorphism, rather than the presence of individuals from two morphologically distinct populations.

An encouraging trend has been the attempts to move away from uni- or bivariate analysis towards various forms of multivariate shape analysis (e.g. see Ruscillo, 2000, 2003). In the end, if a principal components analysis of known-sex modern data simply shows that the males are typically bigger than the females, and fails to reveal any consistent sex-specific differences in shape, then our attempts to apply those results to archaeological specimens will be subject to a high degree of uncertainty.

Over the last two decades, the analysis of ancient DNA has developed from a theoretical possibility to a well-established procedure. One approach has been to identify sequences characteristic of the Y chromosome, and therefore only present in males. Null results present the same problem as counting bacula. If the Y sequence is not identified in the sample, the individual might be female, or inadequate preservation might be to blame. An alternative procedure tests for the amelogenin gene, carried on both X and Y chromosomes, but in a detectably different form on each. There have been a number of successful applications of DNA analysis to determine the sex of human remains (Brown 2001, 307; Stone *et al.* 1996). Nearly all bones from most sites are unlikely to yield the right sequenceable fragments of DNA, and that, together with the resource implications and destructive sampling, will render DNA analysis an occasional, rather than routine, procedure. Its obvious value will be in confirming and validating, or otherwise, the inferences that we draw from more readily-available data. Ancient DNA has been informative in other directions, of course, not least in studies of mitochondrial DNA to investigate the ancestry of European domestic cattle (MacHugh *et al.* 1999).

## And zooarchaeological practice?

What are the challenges for the foreseeable future? One point that has returned repeatedly throughout this brief survey has been the importance of ensuring the quality of modern analogue data. Known-age or -sex data are essential to calibrate the archaeological data, and to give confidence that the inferences drawn from that calibration are well-founded. To put it simply, yet more modern studies are needed to ensure that we really do know what we think we know, including multiple datasets for some of the more widely-studied taxa. Even for the ubiquitous sheep, it is still difficult to decide whether discrepancies between modern datasets have arisen because of inter-observer error, or because of variation between the populations represented by the samples. There are dangers inherent in treating a modern dataset as if those data represent a species, when, in fact, they represent a sample of one or more populations of a species. How well those populations represent the generality of that species is a separate question. On a more subtle point of analogy, the degree of variation represented by the analogue sample needs to be commensurate with what we expect from the archaeological data. A tightly-controlled sample of modern analogue data in which the sources of variation have been minimised will have a particular value, but it might not be a useful direct analogue for an archaeological sample in which the many causes of variation in, for example, epiphysial fusion, have acted to produce much greater individual variation.

Above all, perhaps, the challenge lies where data become information. In order to infer something about the demography of the sample, we have to connect that sample to the population that it represents, and that population to the foraging or husbandry activities of the people whose activities generated the sample in the first place. The first of those two steps might prove to be the more difficult. The sample might represent the demography of a single population at a particular point in time, say over a single year. That resolution of demography might be possible at sites of single catastrophic mortality events, such as kill-sites. In those circumstances, we can define the population with some clarity and confidence, and draw well-founded inferences about the animals and the event that led to their demise. More often, though, the sample is drawn from a heavily time-averaged deposit, and it represents an integration of the fluctuating population demography over an only approximately known number of years. Worse still, if the sampled deposit has a date-bracket of, for example, two centuries, we might not be sure whether the sample represents an integrated demography over the whole of that period of time, or a much shorter period of time somewhere within that bracket. An analysis of age and sex in the sample might be the means to address that question. For example, it can be argued that a Romano-British deposit of sheep mandibles from Victoria Cave, North Yorkshire, is a single-event deposit because of the highly selective mortality profile, even though pottery and coins from the cave indicate human activity over two

centuries or more (Eldridge and O'Connor, in prep.). The mortality profile, with a very high proportion of sheep aged about five to six months, seems unlikely to have been generated by the gradual accumulation of specimens over a long period of time. The potential for a circular argument is obvious, and cases like Victoria Cave need to be tackled with care. However, it demonstrates the importance of establishing the link between sample and population, and it is to be hoped that the next two decades sees us putting more effort and ingenuity into exploration of that link in widely differing datasets.

Then, too, there is the question of modelling hunting and husbandry strategies. The shift of paradigm within archaeology over the last twenty years, away from a preoccupation with process towards a concern for individual agency, has left some of our interpretive methods looking unfashionably deterministic and processual. For our own reassurance, and for the persuasion of other archaeologists, we need to revisit and test some of the models and assumptions that have underpinned our interpretation of age and sex data for years (e.g. Part II of this volume). Are humans optimal foragers? Do predator-prey models give outcomes that match what humans seem to do? Do the conventional models of optimal milk and meat production predict outcomes that actually exist in the archaeological record? If those various models do seem to give defensible results and stand up to repeated testing, then we should use them, and defend their utility. Equally, if they do not then we should admit as much, and develop new models of vertebrate mortality in relation to human activities.

Above all, we should never forget that we are dealing with what were once living animals. They were subject to many causes of variation in their growth and attained adult size, in the rate at which they matured, and in the degree of expression of sexual dimorphism. Their mortality was subject to the human decisions in which we are particularly interested, but also to disease, accident, and misadventure. A great gulf of time and taphonomic processes separates those animals from the bones we study, but the progress that has been made over the last twenty years or so shows that the problems are not insurmountable. In fact, they are not problems, merely challenges.

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*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 9–39*

# 2. Using Osteohistology for Ageing and Sexing

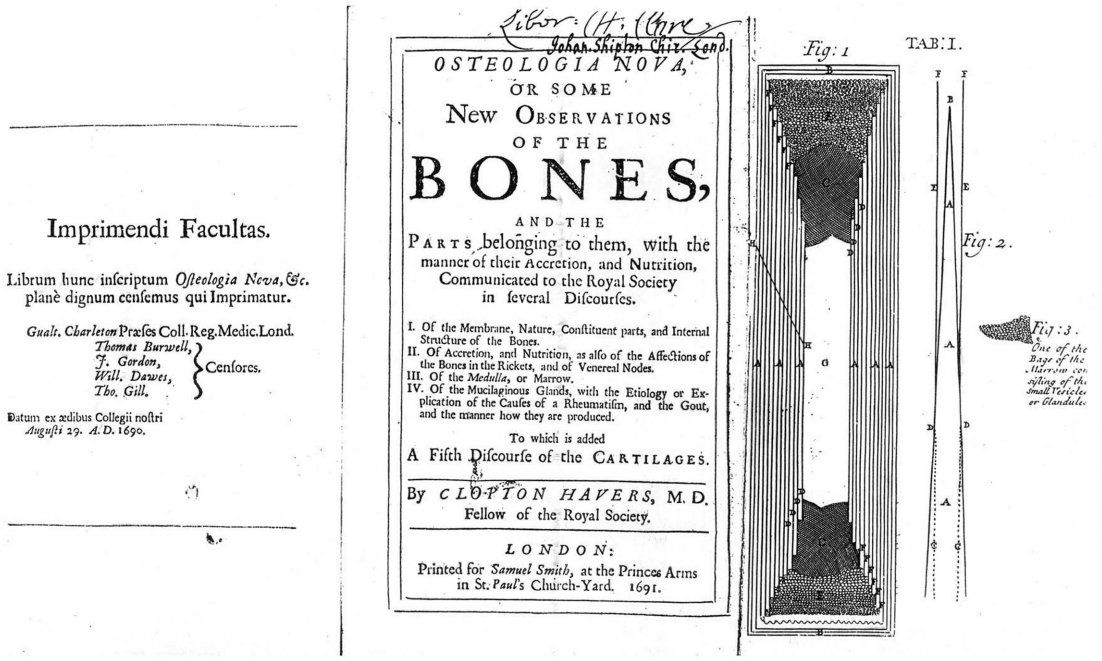
*K. Dammers*

*Microscopic analysis of bones, teeth, and other animal hard tissue can yield considerable information. The most intensively studied of such structures are growth rings and osteons. "Growth rings" accrue to the periosteal surface of many bones as well as in teeth, reflecting annual and shorter periods. Where bone rebuilding has not destroyed them, they can often provide an accurate ageing device despite some problems with readability. The mandible is generally the best bone for this kind of ageing. Various vertebrates have been studied, with differing degrees of accuracy. "Osteons" refers to systems of conduits (and associated structures) for small blood vessels and nerves that grow and run lengthwise in much compact bone of many vertebrates. Osteons respond to the stress and strain of life, and this allows for their use in ageing bones. Various bones, e.g. femur, humerus, and rib, have been used with differing degrees of success and accuracy. Two general approaches are used: quantitative and qualitative. The latter, used in continental Europe, appears to be easier, more objective, and probably more accurate, but both consist of determining the relative frequency or area of various kinds of osteons, their parts and/or their fragments. Much less effective and concerted have been attempts to use osteons for sexing, though under certain conditions this can be done. The methods and techniques commonly used for studying osteons, including the preparation of thin-sections with a microtome or taking of microradiographs, are not very difficult, but they do take some time to learn and to carry out. Advantages of using osteons include their being relatively resistant to fire and other abuses common to archaeological settings, their being able to be studied in small fragments of bones, and their presence in robust bones. Most but not all osteon work dealing with ageing and sexing has been done on human materials. A definite need exists for extending these efforts to more taxa, especially other long-lived ones and ones with marked sexual dimorphism.*

## Introduction

Over three hundred years ago, Clopton Havers (1691) gave the first descriptions of the fine structure of bones (Fig.1). The microscopic analysis of bone structure now provides actual and potential methods of determining the age-at-death and sex of vertebrates. Depending on such factors as the availability of bones and their condition as well as the age and species, histological analysis can be more certain and more accurate than other methods. In addition, it can also be used on material that can not be applied to other methods.

This chapter begins with a summary of the relevant physiology, focusing on osteons and growth rings; explains the principles of sample preparation; gives a survey of histology for determining age-at-death, including methods and results from dental and bone growth rings as well as from osteons; and finally, presents a perspective on using osteons for sexing. The chapter ends with a glossary explaining common terms from osteohistology. Relevant classic and recent literature is presented in the bibliography.



Imprimendi Facultas.

Librum hunc inscriptum *Osteologia Nova*, &c. planè dignum censemus qui Imprimatur.

*Gualt. Charleton* Præses Coll. Reg. Medic. Lond.
*Thomas Burwell*, *J. Gordon*, *Will. Dawes*, *Tho. Gill.* } Censores.

Datum ex ædibus Collegii nostri *Augusti* 29. *A. D.* 1690.

*OSTEOLOGIA NOVA,*
OR SOME
New Observations
OF THE
BONES,
AND THE
Parts belonging to them, with the manner of their Accretion, and Nutrition, Communicated to the Royal Society in several Discourses.

I. Of the Membrane, Nature, Constituent parts, and Internal Structure of the Bones.
II. Of Accretion, and Nutrition, as also of the Affections of the Bones in the Rickets, and of Venereal Nodes.
III. Of the *Medulla*, or Marrow.
IV. Of the Mucilaginous Glands, with the Etiology or Explication of the Causes of a Rheumatism, and the Gout, and the manner how they are produced.

To which is added
A Fifth Discourse of the Cartilages.

By *CLOPTON HAVERS*, M. D.
Fellow of the Royal Society.

*LONDON:*
Printed for *Samuel Smith*, at the Princes Arms in St. *Paul's* Church-Yard. 1691.

*Fig: 1* TAB: I.

*Fig: 2.*

*Fig: 3.*

*Fig. 1. Cover page of Clopton Havers's pioneering work on the microscopic structure of bone. (From a copy at the Göttingen State and University Library, Germany).*

## What Is Osteohistology?

Osteons and osteohistology – the microscopic study of bone – in general, constitute under-utilized sources of information from the fossil record. They can be used in determining taxa, nutrition and diet, stress, limb use, sex, pregnancy, parturition / lactation, illness and injury, age-at-death, and certain environmental factors. This paper presents an overview of actual and potential uses of osteons and other osteohistology for ageing and sexing animals. Of necessity, there are certain generalizations and simplifications.

### What Are Osteons?

Bone is not static: it keeps growing, remodelling, breaking up and dying through-out the life of the individual. Furthermore, bone is in constant physical and chemical contact with other parts of the body, helping maintain its homeostasis. The life-lines of much compact bone are called Haversian canals, the core of so-called osteons (Haversian systems). These canals, about 20–300 μm in diameter (depending on age and species) contain blood, lymph, and nerve vessels, and meander along the long axis of bones. The Haversian canals also send out smaller lateral vessels, known as Volkmann's canals, to provide nutrition to the nether regions of the bone (Figs 2, 3). One can classify osteons in various ways: for convenience, we can think of *primary* (at the beginning), *secondary* (or *replacement* or *remodelled*), and *fragmentary* osteons.

As the mandible, the shafts of long-bones, and other bones grow, new osteons burrow through, insuring the effective transport of nutrients (Fig. 2). The canals are formed by osteoclasts (destructive cells) boring through the established bone by "resorbing" it, affecting primary bone, primary osteons, or other secondary osteons, making a cone of construction in front of the vessel. Osteoblasts (constructive cells) then line this cone and secrete mineral-building substances, turning it into a tube of minerals. This lining is said to consist of a lamella, 3–20 μm thick made up of collagen fibres, *ca.* 0.06 to 0.6 microns in diameter. Over time, other concentric lamellae form inside the first, the outer edge of which has a distinctive cement ring. Thus, a cross-section of a secondary osteon consists of blood, lymph, and nerve vessels, and perhaps up to seven to 20 lamellae surrounding the canal. Within the lamellae are lacunae: generally oval-shaped spaces with osteocytes trapped in them but connected to each other with a fine web of canaliculi containing their connective processes and the central canal but not extending past the cement line.

The presence, frequency, size, shape, etc. of osteons and their constituents will vary according to species, type of bone, and location along the bone shaft. Other factors affecting osteons are whether they occur near the core or exterior of the bone, as well as age, season, sex, stress, diet, injury, disease, and taphonomy (for archaeological bone).

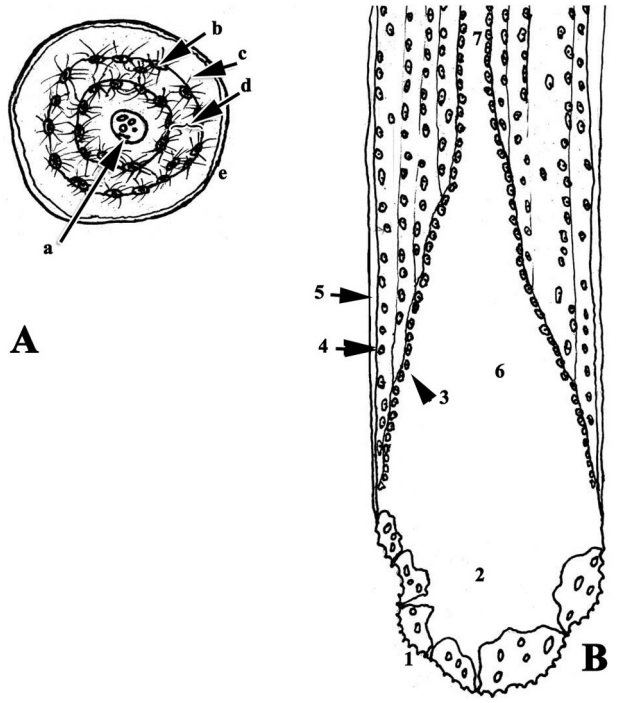



*Fig. 2. Schematic of osteon.* ***A****. Cross section. Indicated are Haversian canal with blood and lymphatic vessels, a nerve, and loose connective tissue (a), osteocyte (b), canaliculus (c), lamella (d), and reversal line (e).* ***B.*** *Formation shown in longitudinal section (line of advance is downward). Indicated are osteoclast dissolving old bone (1), cutting cone (2), osteoblasts being deposited (3), osteocyte (4), reversal line (5), closing cone (6), and Haversian canal. (Adapted from Kardong 1995, fig. 5.26, Robling and Stout 2000, fig. 7, and Walker and Liem 2000, fig. 6.9).*

### Change in Osteons

As the body continues to grow and age, various physical and chemical stresses and strains play upon the compacta and its component osteons. The lamellae, forming concentric rings around the Haversian canals, gradually close them off, like a calcified water pipe. Replacement (secondary) osteons cut through the old ones, leaving osteon fragments, like the wreckage of old drainage pipes beneath the streets of a city. The amount and area of both the replacement osteons and fragments, as well as resorption lacunae, generally increase with age. Not surprisingly, different bones and bone locations, in populations and sub-populations (such as sex) have different stress factors, which are reflected in osteon assemblages. These are "biographies": the moving finger having written, moves on but it leaves behind its message.

Not all mature compact bone is characterized by osteons. Some bones in animals have different structures, moderately correlated with gross taxon (e.g. horse or reptile) as well as bone function and rate of development. Thus, plexiform bone is formed in rapidly growing long bones that need to endure heavy stress. Oddly, this structure does not necessarily entirely preclude the presence of an odd osteon or, following Wolff's Law of stress response, of clusters of them in strategic locations (at least as time passes). In addition, there can be layers of lamellae that can be added to the inner and outer bone surfaces; these layers are discussed below, in the section on ageing.

I also want to consider an even finer scale for a brief moment before turning to lab techniques and ageing and sexing. The molecular level of bone, in particular osteons, is active. It is also not completely understood and has suffered, as has histology in general, from a seldom-broken focus on a limited number of species (especially rats and humans). In any case, the standard model holds that within a few weeks after initiation, e.g. due to an injury or accumulated microfractures, a completely new secondary osteon will be formed by the construction crew (the BMU: bone remodelling unit). This unit consists of the osteoclasts with acidic mineral-dissolving secretions and is followed by the osteoblasts laid down along the walls of this advancing cone. Some of the osteoblasts get trapped and become or get designated as osteocytes. The nutrient supply lines, with blood, nerve, and lymph vessels, follow. The osteocytes are attached to the vessels in the heart of the canal via extremely small vessels called canaliculi, and thereby supply the bone with its necessary life-giving provisions. After a while, a new lamella gets laid down by osteoblasts, with lacunae occupied by further osteocytes (old osteoblasts). In some places, lateral sub-canals branch out, never into any other living secondary osteon, but sometimes to the bone surface. And so it goes, until the concentric lamellae close off the canal or a new demand calls for rebuilding and the BMU cuts through the established osteon. In humans, a new osteon can lay down 70% of its mineral structure in a fortnight or so, and be completed in 100 days, while completion in a cat takes 50–90 days (Pritchard 1972). While turn-over is said to be about ten percent per year, the natural life-span of a secondary osteon is variously said to be about a decade and a half to a quarter century. For a more detailed but still archaeologically orientated discussion of osteon histology, see Robling and Stout (2000), especially pages 187–190. Other detailed descriptions, including those of the molecular and chemical processes involved, can be found in bone physiology texts such as Bloom and Fawcett (1975), Caplan (1998), Martin *et al.* (1998), Kingsley (2001) and Currey (2002), or the multi-volume reference work edited by Bourne (1972).

As indicated above, in some dense bone, Haversian systems are absent or rare. Here, the nutrients are supplied differently. The most prominent dense bone that is non-osteonal is plexiform bone (though there can be some, usually scattered, osteons in this kind of bone; see Fig. 4). Plexiform bone is so called because of the vascular plexuses (an interwoven combination of elements in a

*Fig. 3. Cross-section schematic of long-bone microstructure. Indicated are (A) line of arrested growth, (B) primary osteon, (C) line of resorption, (D) Volkmann's canal, (E) resorption lacuna, (F) interstitial lamellae, (G) secondary osteon, and (H) trabecular bone.*

cohering structure) contained within lamellar bone between non-lamellar bone (Martin *et al.* 1998). It has been described as "bone in which the lamellae are grouped into layers separated by well-developed vascular channels or by bands of osteons" (Sheffield, no date). In cross-section, it generally looks like corrugated cardboard that has been fan-folded. This structure is observed in many bones exhibiting rapid growth, e.g. equid long bones. Plexiform structure can occur at certain locations, e.g. the diaphysis of a bone. Some birds have what could perhaps best be called plexiform structure, though it is a bit aberrant. The structure is generally absent from most living reptiles.

Other dense bone can be acellular or even non-vascular, so that much of many bones of specific vertebrates (e.g. marsupials and insectivores) is non-Haversian.

### *What Are Growth Rings?*

On many animals (and practically all mammals if not vertebrates), the hard structure adds periodic layers to its surface, giving an appearance similar to the familiar rings in trees (Fig. 3). These lines/layers/rings are similar to tree rings in that they reflect, to a certain extent and insofar as they are not obliterated by remodelling, 1) periodicity (useful for ageing), and 2) stress (useful for ageing and sexing). Among the hard tissues which exhibit these predominantly microscopic accretions are long-bones, ribs, and mandibles of a number of mammals and reptiles. Turtle scutes, mollusc shells, otoliths, scales, tusks, teeth (dentine, enamel, and cementum) and antlers also exhibit periodic layers. I will go into the causes and meaning of these so-called recording structures or growth rings in the section on ageing for bones and, briefly, for teeth. These lines are caused by (changes in) stress, feeding, parturition, nursing/lactation, and other behavioural cycles, internal biochemical triggers, and by external cycles. Stress comes in many forms, some of the important ones being the transition from intrauterine life to that in the external world, the onset of puberty, sexual activity, midlife change, and death. In addition, diet, exercise, injury, disease, and seasonal weather vary the stress on animals in ways that can be reflected in the fine structure of the hard tissue.

Generally, incremental growth markers can be can be divided into two types: bands and lines. The broad bands represent rapid growth, whereas the thin lines reflect slow growth, e.g. during hibernation or between feeding periods, when deposits build up almost on top of each other. In a sense, feeding is a source of stress. In any case, daily feeding/rest cycles are reflected in dental lines, while longer cycles (especially in some hibernating animals) are more dramatically seen in hard-tissue growth-ring patterns. Hard winters (and/or the dietary difficulties caused by them) provide us with winter growth ring patterning in cervids and some other temperate, sub-arctic, and arctic animals, while wet/dry seasonal patterns are reflected in the bones of lower latitude grazers and reptiles. But even in less fluctuating climates, there *appears* to be an annual pattern in at least some animals visible to researchers, e.g. weekly and sub-hibernating cycles.

The suprachiasmatic nucleus (SCN) (Ohtsuka-Isoya *et al.* 2001), a part of the brain that regulates various circadian rhythms, has been demonstrated to play a crucial role in growth ring production. These various factors interact, e.g. sickness and health, as the organism varies its diet, sleep, sex, and other patterns in order to protect the body and live. While this interaction makes for more difficult interpretation, since the various "texts" (osteons, bone growth rings, and various dental growth rings) are "written" by differing combinations, a composite analysis can theoretically reveal many a sub-text. Thus, while this chapter deals with age and sex, the investigator needs to keep in mind the environment, health, etc. of the individual while doing an analysis.

With growth rings, there can be a certain amount of error in the reading. In part this has to do with the experience and lab tradition of the researcher, as well as the equipment, but other factors play a role as well. Important among these are the variability of growth rings (disappearing, single, splitting, double, [Klevezal 1996, 61–70; O'Brien 2001, 50]), the differences from bone to bone and from locus to locus on a bone and even around a single cross-section. For each category and for each species, and even macro-environment, each lab needs to set up a reference series so that other workers can make comparisons. For example, standards from the useful work on mammals in Russia carried out by Galina

Klevezal can be compared and applied to Canadian material. Still, researchers are already at the point where for many taxa (most mammals found in Russia, crocodiles, and many amphibians and cetaceans), major bone growth rings can be taken as effective annual or bi-annual markers except in long-lived species. In these cases, bone turn-over destroys at least some rings, but dental annuli are effective on the daily and annual level and have even been reported to have weekly and monthly variants (Klevezal 1996, 70–80). The preferred location for bone growth-ring investigations is on the mandible just below the ramus, while molars or canines cross-sectioned near the gum line are the best selections for most teeth. Osteon changes are best seen mid-shaft on the tibia, femur or humerus, with the ribs also having some value. Mandibular readings have not proven to be very good in larger mammals, but in smaller animals they hold out some promise of perhaps being equal or superior to long bones for supplying useful records.

## Sample Preparation

### *Introduction*

The two most common research uses of fossil or archaeological osteons and other microstructures are taxon determination (e.g. Máytás 1927; Amprino and Godina 1947; Enlow and Brown 1956–58), and ageing (e.g. Yoshino *et al.* 1994, Klevezal 1996, Robling and Stout 2000). Once the bone and taxon have been determined, samples can be examined for ageing (and/or other fields of interest such as sex, disease, injury, and environmental influences/reflection). While what follows is directed specifically at the examination of bone for osteons and growth rings, at least the general principles are applicable to the histological study of other hard tissues.

The procedures for preparing samples for study are similar, independent of sample or research question, as long as one is using thin sections and a standard microscope. Variations occur primarily with the stability of the available bone and which observation methods are to be used. This is especially the case in choosing between "blind" approaches that are relatively rigid (in order to be consistent and objective) and "choice" approaches which require the researcher to select an appropriate field of view.

### *Sampling*

If a *population* is being sampled, two prime considerations are to be observed. First, the sampled material must be of adequate quality. Unfortunately, this cannot always be determined before processing, though general appearance is a rough guide and can be greatly assisted by a knowledge of the local taphonomic conditions. The second consideration is to follow usual statistical and sampling procedures.

If an *individual* is being sampled, an appropriate bone should be selected. In most species, the bones found to give the best results are the femur, humerus, tibia, and to a lesser extent the ribs, for osteons. For growth rings, extensive successful research on the mandible makes it the current bone of choice. While taking numerous samples from a single bone has been legitimately encouraged (e.g. Harsányi 1993), it seems that this is not normally necessary (Robling and Stout 2000; Klevezal 1996). Instead, one location at about midshaft should generally suffice. The sampling technique will determine whether a disk or more restricted shape (plug or shaft) should be taken from the bone. Limited disposability of a bone also restricts the shape and amount of the sample taken. If possible, a disk-shaped sample is preferable because it provides all possible loci and rings and is thus applicable to all analytical techniques. The section should be taken perpendicular to the long axis of the bone.

### *Physical Preparation*

Once the area to be sampled has been chosen, the slice is removed from the bone with a fine hacksaw or band saw. The slice should be about a centimeter or a half a centimeter thick. It is then embedded in resin (balsam) to keep it stable, whether it is fossilized or not. After a full day to harden, the block is then put on a special cutting machine called a microtome and cut to the appropriate thickness (*ca.* 30–80 microns), creating a smooth surface. The slicing takes a few minutes, depending on the size and hardness of the bone. The sample is now ready for mounting on a slide, depending on the observation method. This is the method used in most better-equipped labs. It requires very little skill; however, microtomes are costly. An alternative approach presented by Maat *et al.* (2001), requiring no expensive equipment and producing better quality samples, requires somewhat more skill and practice. Basically, in twenty minutes a hand-ground sample of the highest quality will be produced. Other guides to preparing the slides include Chinsamy and Raath (1992), Wilson (1994), and Pfeiffer (2000, 289–90). For dental samples, see Beasley *et al.* (1992).

The most frequently used method to examine the samples for growth rings or osteonal structures involves an optical microscope with transmitted light and an adjustable polarizing (birefringent) filter, at magnifications from about 30× to around 200×, depending on species, etc. In this case, the sample is simply mounted untreated on a slide, usually without any hues, though a few researchers use various stains, such as light red Gram-Weigert, toluidine blue or basic fuchsin. Teeth, especially if demineralized, are normally stained, with haematoxlin or toluidine-blue (see Klevezal 1996, 5–13). On the other hand, O'Brien (2001, 47–8; see also Lieberman and Meadow 1992, 59–69 and Stutz 2002) argues that teeth studies should use the following standard procedures in order to get results that truly reflect annual growth rings:

undecalcinated teeth should be embedded in a fixative and petrographically thin-sectioned without staining before being examined. A transmitted-light microscope using cross-polarized light should be used to examine the acellular cementum. The increments are then defined on the basis of refractive properties. In fact, the alternating lines are not always clearly distinguishable, at least for the novice even with the cross-polarized light, though O'Brien (2001) claims a consistency and accuracy of readings.

Alternative viewing possibilities that have been used are reflective light microscopy, SEM, microradiography, and scanning acoustic microscopy (Katz and Meunier 1993; Brandt and Klemenz 1998; Eckardt and Hein 1999; Katz and Bumrerraj 1999; Smitmans *et al.* 2000). For SEM, acid etching of non-fossil material can improve differentiation. Finally, some researchers have begun producing three-dimensional images of osteons by computer image manipulation of stacked slices (Stout *et al.* 1999), direct-reading of sliced-off surfaces (Constans 2001), CT scans (Pattijn *et al.* 1999; Fajardo *et al.* 2002) with a resolution of 60 microns, and non-destructive X-rays down to two micron detectability (Tappen 2001; Skyscan, no date). While these advanced techniques provide a more realistic and complete picture of bone histology – at least at the osteon level – they have yet to be incorporated into the interpretive body of knowledge based on our "flat-earth" model. Still, they bode a revolution, even though they are not (yet) of the high resolution that cross-sections are and are not capable of presenting all relevant details. Even finer studies, focusing on third order, or ultrastructure, such as atomic force microscopy (Henning *et al.* 1999), are just now being applied, as is Raman spectroscopic imaging (Timlin *et al.* 2000).

Once the section has been fixed for a microscope slide, it can be examined with any number of devices: reflected or transmitted light, SEM, SAM, STM, AFM, etc. As stated above, though, the most common approach is to use transmitted light with a variable polarizing lens. Because using polarized light takes a certain amount of fidgeting and since different viewings can provide different information, most investigators prefer to work with the original material, although a minority prefers the objectivity of a fixed photographic image. For qualitative and growth ring work, a low resolution (perhaps 10×–20×) is first used to scan for an area that has not been disturbed by anomalies, such as those caused by injury, disease, muscular stress, taphonomy, or the lab dog. When a good area has been determined, then a magnification of about 50× to 100× (or more for growth rings in some taxa, and for tooth enamel and dentine 70× to >250×) is selected and the polarization can be tried out. The slides should of course be clearly and systematically labelled to include all relevant information concerning the source: a histological sample without adequate documentation is about as useful as a sherd or flint chip without provenience. If feasible, remaining bone or a significant portion of it should be retained with the sample. This is especially important if one chooses to work with images rather than physical samples.

*Fig. 4. Cross section of sheep's long bone showing primarily plexiform structure with some primary osteons, especially at bottom of picture. (From Demeter and Máytàs 1928, fig. 85; © Springer-Verlag).*

## Determination of Age-at-Death

### *Introduction*

The living world is ruled by three clocks: that of the sun, of the moon, and of the earth. Most clearly laid down in animal hard tissue are the marks of the sun, that is, the annual record. Next come those of the earth. The smallest astral body, the moon, lays down the most controversial and some of the most precise of these marks: menstrual and estrual stress markers on the one hand and tidal markers on the other. Yes, even tidal markers with ages reflect changes as fine as a half day or so. Furthermore, the moon in its four phases (or the 6.6 day cycle of solar radiation) could be related to the weekly records that some researchers have reported! Besides these forces, which leave their records as incremental marks, there is the less precise but more robust Haversian system, which can be used as well, especially when the growth rings are defective, missing or ambiguous. It can also be used as a check on the growth-ring records.

### *Growth Rings*

Various researchers have demonstrated that the hard tissue of molluscs and practically all vertebrates have annuli, rings or lines that reflect annual and sometimes even finer cycles. Annuli can be found in fish bones and scales (Menon 1950; Das 1994), amphibian bones (Enlow and Brown 1958), reptile bones (Horner *et al.* 1999), tusks (Fox 2000), enamel, dentine, cementum and mammal bones (Klevezal and Kleinenberg 1969). In these rings are recorded the individuals' responses to weather (hot/cold, wet/dry) and the effects of hibernation, as well as dietary, sexual and monthly stresses, mediated through an internal clock that seems to have incorporated at least days (*ca.* 25 hours) and years. The general pattern consists of a growth ring (or recording structure) consisting of both a growth zone (in which rapid growth produces a wide band), and an adjacent narrower band representing either no outward growth (line of arrested growth: LAG) or markedly slowed growth (annulus). An annulus can contain one or more LAGs. Ideally, there is one clearly defined growth ring per time unit – usually a year. These get added on centrifugally to the periosteal surface.

Some taxa can present various problems such as filled pulps precluding ageing of older individuals, eroded cement, lack of teeth, resorption of adhesion lines in bone, or accessory and double lines. Despite these difficulties, Klevezal and Kleinenberg aver that "the method for determining the age of mammals according to the number of layers in the tissues of tooth and bone is the most universal and accurate" (1969, 109). This perspective seems correct to me and, *mutatis mutandis*, applicable to most other hard-body animal taxa in polar, temperate, rainy/dry, and, less auspiciously, in monotonic climes.

#### *Dental Growth Rings*

Dental growth rings are usually the most detailed and, in general, give the finest-tuned record of growing older. Although teeth are not the focus of this article, the following is a very brief introduction to these related phenomena. For an overview, see Carlson (1990, 542–4) or Pike-Tay *et al.* (1999, 297–301); Reid (1997a) for dinosaur histology; for mammals, see Klevezal (1996, *passim*); and for an archaeologist's bibliography, see Gordon (1984 and 1992).

Most mammalian teeth can be said to have three kinds of hard components, each capable of providing recording structures. Starting on the inside is dentine, a 35% organic material that grows inward in curved waves, gradually filling up the core of the tooth. The lines of dentine can have various meanings, depending on location and other factors. Enamel forms the visible part of teeth. It is very hard, being 96% percent mineral (Klevezal 1996, 15–6). The part of the tooth that attaches it to the jaw is fittingly called 'cementum,' a 50% inorganic material. "The physical and optical expressions of growth increments in teeth are due to differing patterns of collagen fibre organization and to cell content / degree of mineralization" (Pike-Tay *et al.* 1999, 298) and crystal orientation. For an explanation of the complicated microstructure and sample preparation of teeth, see Hillson (1986, 107–75); Lieberman and Meadow (1992, 59–69); and Klevezal (1996, especially 16, 24–48 and 70–80).

Half a century ago, V. B. Scheffer (1950) began studies on pinniped dental growth layers. Laws (1952 and 1953) then used pupping season-related rings of alternating columns and marble dentine to age elephant seals' canine teeth of up to twenty years to within one month. He also did preliminary work on other mammals that other people, especially Klevezal and her associates, have since developed in detail, and extended studies to enamel and cementum. Enamel is now the material most commonly used for ageing mammals with growth rings. It is believed that "mammalian dentine universally shows circadian increments" (Ohtsuka-Isoya *et al.* 2001, 1364). Dentine has been demonstrated to lay down observable increments on an approximately 24-hour cycle in rabbits, rodents, humans, pigs, and other mammals, influenced or controlled by the brain's suprachiamsmatic nucleus (Ohtsuka-Isoya *et al.* 2001). Klevezal (2001) reports that incisors in female mice have clear daily lines in the dentine (see also Trunova 1999 and Klevezal). Fine lines of alternating high and low transparency, apparently reflecting differences in mineral content (Klevezal 1996, 38), are laid down starting before birth. Heavier demarcation reflects longer-termed periods and isolated events such as circumnatal trauma. Unfortunately, the dentine growth, which advances in an inwardly filling manner at rates per day of 12–24 μ in voles and 1.9–3.9 μ for mice (Klevezal 1996, 12), can completely fill up the tooth and then stop recording, sometimes as early as the onset of maturity.

Finding tooth sections with lines actually *recording* rhythms rather than frequent multitudinous individual variable or non-recurring events is difficult (Klevezal 1996, 155). Thus, dentine has not been used much in ageing terrestrial mammal teeth (see Table 5 in Klevezal 1996, 54–9; see also Hillson 1986, 223–9, for an archaeological perspective). Work using this technique does continue, however, including successful daily-line readings in mice incisors (Klevezal 2001), hibernation markers in 17 species of rodents grouped into three patterns (Trunova and Klevezal 1999), and Russell's advocacy for its use in humans (1996). Additionally, Fox (2000) claims to have identified yearly, weekly, and daily incremental growth lines in gomphoteria from the Miocene. Other studies reported in the literature include Miani and Miana (1972) on dog dentine as well as Okada and Mimura (1941) and Rosenberg and Simmons (1980) on rabbits. The latter produced easily identifiable images of daily increments (Fig. 5). One other group of animals where dentine has been used is bats, creatures that otherwise are quite a difficult to age. Their dentine

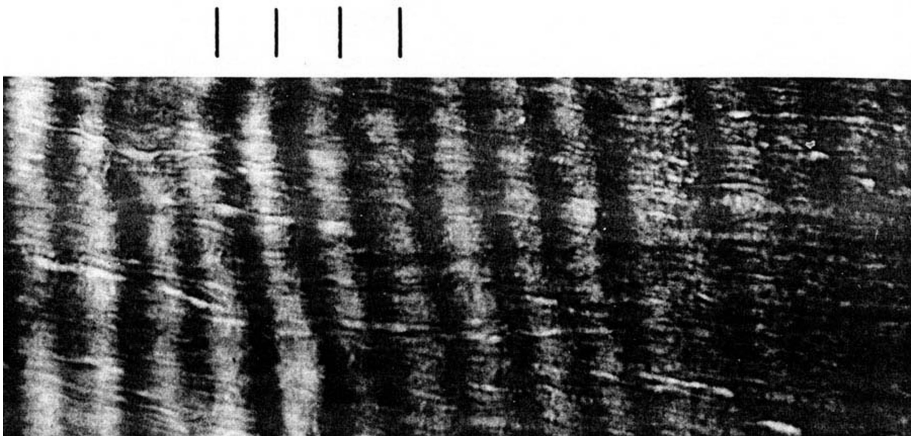


*Fig. 5. Stained and decalcified rabbit incisor dentine showing daily increments. Each pair of dark and light bands, indicated by the lines above the photomicrograph, is about 20μm in width. (From Rosenberg and Simmons 1980, 32, fig.1A; © Springer-Verlag).*

incremental lines are often observable, and represent a conservative minimum age in years that is, unfortunately, characteristically well below actual age (Batulevicius *et al.* 2001; Batulevicius, pers. comm.).

The histology of enamel is visually clear (Klevezal 1996,15–6) and also seems to reflect an acid/neutral alternation (Takagi *et al.* 1998). In principle, it is a good recording medium; however in practice, enamel often fails due to attrition, resulting in the loss of recording structures. The daily bands are also complete at eruption (Klevezal 1996, 14). Thus, its application is pretty much restricted to young individuals, where some of the permanent teeth are not yet complete. On the other hand, *where* applicable, daily increments have been claimed to be quite readable, even though some oral biologists deny the very existence of incremental lines (for discussions see Klevezal 1996, 15–6; Hillson 1986, 119–27; Ramirez Rozzi 1998)!

As mentioned, cementum is by far the most popular source for obtaining growth rings in ageing mammals (for methods see Beasley *et al.* 1992 and Stutz 2002; for surveys see Stallibrass 1982 and Klevezal 1996; for a simple explanation and archaeological references, mostly to seasonality, see Pike-Tay *et al.* 1999, 297–305 or Lieberman and Meadow 1992). In fact, according to Peabody (1961, 12), in 1860 Hittel noted cementum layers in California grizzly bears and called for experiments in mammals to confirm their presence. A century later, Smirnov (1960) undertook such studies, examining some carnivores and rodents, complementing work that was being done on marine mammals at about the same time. Of the histological areas, cementum usually gives the most correct and reliable ages, though not particularly the most precise. It is particularly advocated for use in carnivores (King 1991, 31; Klevezal 1996, 106), and its use is popular in ageing ungulates as well (Klevezal 1996, 58–9; Lieberman and Meadow 1992). For carnivores, the canines are preferred, whereas in the ungulates incisors and molars are used. On the other hand, about a quarter of sheep ages were reported as being erroneous by more than a year. The "crystalline orientation and/or size is responsible for the layered appearance of cementum" (Cool *et al.* 2002, 386), which can be read accurately as reflecting years, though advancing age and double lines broaden the estimate to about 5%. Klevezal notes that the "pattern of growth layers in cementum is usually simple…, [consisting of] a band of tissue and an incremental line," which looks pale in transmitted light and dark in reflected light (1996, 39). Most of Klevezal's data on growth rings, both her own work and that of others that she discusses, focuses on the effective ageing using cementum in most groups of northern mammals (see 1996, Table 5, pp. 54–59 and Chapter 6, pp. 124–177, and more recently Klevezal 2002). O'Brien (2001), in reviewing the literature on African cementum studies, concluded that, where the standard procedure (presented in the previous section) is used and annual increments are taken as a combination of one opaque (dark) and one translucent (light) line, good results are obtained for zebras and other tropical mammals.

Specific studies include Klevezal's previously mentioned study of mice (2001), which also reported on cementum. She noted that winter incremental lines in the molars not only could be used as an indication of over-wintering, but that the amount of growth on either side could narrow the age estimate. White (1974) studied roe deer using a 20× reflected-light microscope to examine sections he had ground smooth with very fine carborundum. He observed clear and regular repeating pairs of opaque and translucent lines, the pairs matching the number of years lived. Preparation and evaluation, described in detail, took thirty minutes per tooth. In the

discussion section, the author notes that earlier studies indicate that the teeth of roe deer associated with a demonstrably milder winter and higher quality of food do not show winter markers. Pike-Tay (1995) noted that seasonal markers on caribou teeth were made difficult to read by a number of factors, including specimen preparation and variations in feeding (see also Miller 1974 and Pike-Tay 1999). McKinley and Burke (2001) found that cementum on horse teeth could be read with only minor, resolvable, inter-observer variability, and produce accurate results. A study of wildcats proved effective to closer than one year, though with the caveat that 7% of the animals had an additional (but identifiable) "kitten" line (Garcia-Perea and Baquero 1999). The first real line develops at nine months. Not so confident were the results of an extensive study of fishers that questioned accuracy on individuals three years and older, noting that similar difficulties for other fur-bearing animals had been pointed out in the literature (Arthur *et al.* 1992).

Studies on various primates have given good results for molar cementum. For example, Kay *et al.* (1984), studying eight wild-living macaques of known ages, concluded that around 90% of the ages could be correctly made, making cementum measurements "the most accurate method for aging skeletally adult primates [yet to be] tested on animals of known age" (85). On the other hand, long-lived species can be problematic. Condon *et al.* (1986) report errors averaging six years using a modern population of geographically restricted *Homo sapiens*, using cementum annuli. This is hardly the "to the day" accuracy reported by some independent researchers, especially in other species (329). In addition, Condon and his co-workers note that inaccuracy increases with age in a number of cervids (moose, red deer, and Virginia deer) (328). In his recent book, O'Connor notes "an uneasy consensus emerging that cementum increment counts are an acceptable estimate of age in some species," especially when used on individuals that have not reached later adult ages (2000, 82).

Closing on dental growth rings, we note their general effectiveness, with each kind having advantages (dentine: fine scale, early start, protection from destruction; enamel: effective in young and even prenatal studies; cementum: continues for all or almost all of life). The limitations must also be recognized. Key among these are: dentine can fill the pulp cavity and thus stop recording; enamel is restricted to ageing younger individuals, and outer layers can also be lost by wear; cementum can be resorbed, be covered with calcium build-up, sometimes has double layers and other reading problems, and the winter line appears to be absent in non-stressed conditions on some species. Finally, each is subject to its own diseases which mar recording. Even though there is a general retrenchment (Darius Batulevicius, pers. comm.) from some of the euphoric claims that have been made in the past, to a considerable extent this retrenchment has been brought about by inconsistent and less than optimal testing methods (McKinley and Burke 2001). Careful development of controls should continue to bring us closer to highly accurate ageing where good tooth samples are available.

*Bone Growth Rings*

The bone building crew (BMU: bone maintenance unit) has workers all over, including on the endosteal (inner) and periosteal (outer) surfaces of the bone. On both of these surfaces, osteoblasts, apparently receiving orders from nearby monitoring osteocytes (Moskilde 2001, 152), lay down organic material that later becomes mineralized by deposition of hydroapatite crystals. Given the right conditions, this apposition will appear in the form of layers, analogous to tree rings or cementum growth rings. These are called circumferential lamellae. This process is very complicated, and its workings are still a somewhat controversial matter (see Klevezal 1996, 17–23). The growth rings will normally form if, when, and where, a slowing of growth allows a concentration of mineralization and/or change in orientation of the crystals. When growth is rapid, it is in fibro-lamellar form; when it slows, pure lamellar structure can form. Not all bone will have these bands. For example, load-bearing and fast-growing bones and fast-growing species rarely exhibit them (at least in the loci so far investigated), especially since the bone tissue is not rarely plexiform. Although apposition continues throughout life (Klevezal 1996, 18), it slows coincidentally with slowing in skeletal growth. At this point, growth rings are more likely to be visible, although in long-lived species, rings late in life can be absent or almost piled up on top of one another. Unfortunately for the annuli-bedazzled archaeologist, the bone-building crew does not stop once the circumferential lamellae are laid down. Just like city planners redirecting municipal services to dig up newly laid street surfaces to put down new water or gas lines, new service lines – secondary osteons – remodel the bone, often including the growth rings. But that is another matter discussed below. Where the resting lines are intact, with a so-called reversal line marking the limit of reconstruction, they are taken (based on extensive research) to reflect annual periods of relative rest in growth during the winter or dry season. To what extent this periodicity is due to an internal clock controlled by hormones from the SCN (for example) or to the environment has yet to be fully understood. Bone growth rhythms probably evolved in synchronicity with the seasons, though the evidence seems to support the usual flexible mix of nature and nurture. Because of geometric conditions, the endosteal (medullar) surface growth rings are more constrained and generally less useful for ageing. In some taxa, finer than annual increments have been reported, but in most species, extra lines represent artifacts (in the sense of *Störfaktoren*). "Periosteal bone tissue as a recording structure is, in general, characterized by high sensitivity and small period of record persistence. Because of that it is the least

convenient" of annuli to use for ageing given variations due to environmental change and injury (Klevezal 1996, 106). On the other hand, it is useful in vertebrates without useable teeth-structure and in individuals with no remaining or serviceable teeth.

The following is a short overview of some of the findings of periosteal growth rings.

*Fish*. The use of otoliths for ageing and seasonally identifying various fish is generally effective and well known (e.g. Victor and Brothers 1982; Van Neer *et al.*, 2002a). The annuli can reflect daily cycles, perhaps of feeding and/or light, so that otoliths can provide extremely fine ageing – down to the day – and, maybe even the time of day of the kill! There are, however, problems of misreading due to false, hidden, and missing annuli (Victor and Brothers 1982). Otoliths are also not as commonly recovered from archaeological sites as vertebrae. Fortunately, these bones also have growth rings that can also be used to age fish, though not as well as otoliths. For discussions of fish vertebrae and other non-otolith bony materials for ageing and seasonality, see Menon (1950) for an extensive though old survey, and Van Neer (1993: clariid pectoral spines), Van Neer *et al.* (1999: plaice) and Dubick (2000: eagle ray) for recent specific and critical work.

*Amphibians.* Castanet (1975) and others have also found acceptable growth rings for amphibians. Examples include golden-striped salamanders (*Chioglossa lusitanica*), where annuli appear to be laid down yearly, and are different after metamorphosis (Lima *et al.* 2001). A northern species of salamander could be aged within two years of actual age, with no resorption difficulties seen in the older individuals (Smirina *et al.* 1994). In various anurans, growth rings in *digits* as well as in the femur were effectively used (Sullivan and Fernandez 1999; Erişmiş 2002). Fig. 6 gives an example of how these growth marks look in a stained decalcified cross section. A recent study of sixty-two Indian frogs (*Microhyla ornata*) produced consistent, almost perfect, results for many bones in both sexes and all ages, thus showing that extreme seasonal temperature swings are not necessary to produce meaningful growth rings in frogs (Kumbar and Pancharatna 2001). On the other hand, Smirina and Makarov (1987) emphasized the effects of climate on resorption in the grass frog (*Rana temporaria*). Esteban *et al.* (1996) also caution that 7% of the 103 Spanish frogs they studied showed weak, unreadable winter markings. Other amphibian studies, with generally the same results, have been reported in Schroeder and Basket (1968), Kleinenberg and Smirina (1969), Smirina (1972), Castanet and Roche (1981), Guyetant *et al.* (1984), Castanet and Smirina (1991), and Smirina *et al.* (1986). Caution should be exercised, however, as a number of these studies note that in some species resorption of inner growth rings can lead to deceptively low readings, especially for the untrained observer (Kumbar and Pancharatna 2001).

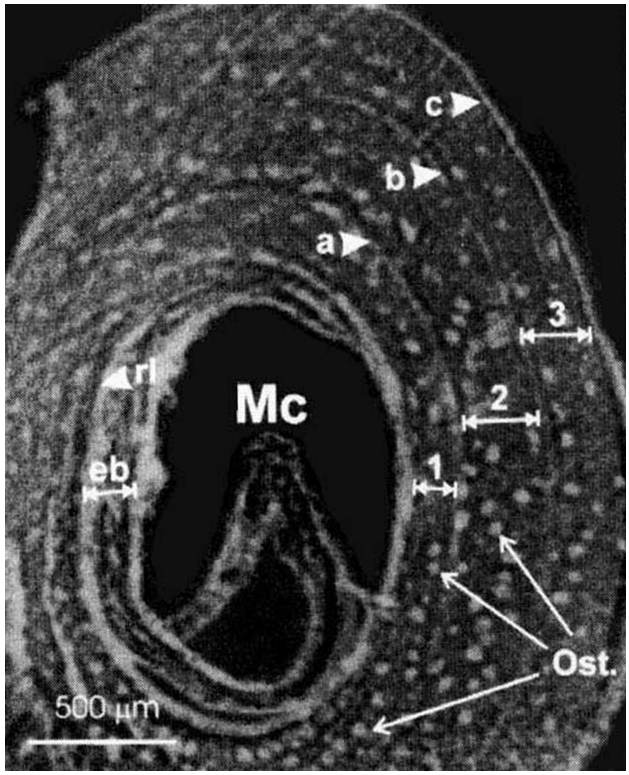



*Fig. 6. Cross section of femur of a water frog (*Rana bedriagae*). Indicated are lines of arrested growth are (a-c), growth zones (1–3), osteons (Ost.), resorption line (rl), endosteal bone (eb), and the medullary cavity (Mc). (From Erişmiş* et al. *2002, figure 2; © Turkish Journal of Zoology).*

*Reptiles.* There is extensive and sophisticated literature on growth rings in dinosaurs (e.g. Nopsca and Heidsieck 1933; Reid 1990, 1997; Chinsamy 1993; Horner *et al.* 1999), which has helped advance interpretive histology. Other reptiles have been reported in some detail as well (e.g. Bryuzgin 1939; Warren 1963; Castanet and Smirina 1991; and, for a Permain genus, Ray and Chinsamy 2004). Donald Enlow, the leading comparative osteohistologist of the mid-century, gave an overview of bone growth rings for ageing reptiles which is largely applicable to other vertebrates. He came to the conclusion that, while growth rings can provide extensive data on past circumstances of growth and broad-band *relative* ageing, they are apparently not useable for absolute ageing. The confounding factors he listed are: 1) the problem of resorption, 2) the presumed reflection of seasonality of annuli inconsistent with tropical and temperate snakes showing similar patterns, 3) only certain loci having rings, even on the same elevation of a bone shaft, one side frequently having more laminae (1969, 63–68). While these factors preclude a simple application of a one-to-one correlation of laminae with years or over-

wintering, further studies have shown that a careful understanding of individual species *does* provide fairly accurate quantitative ageing in a number of cases (Castanet and Smirina 1991).

Bone growth rings in crocodilians have been extensively studied (Buffrénil 1980; Buffrénil and Buffetaut 1981; Hutton 1986). Crocodiles show clear annual growth rings, although those held in monotonic environments and provided with an abundant diet exhibit decidedly *less* marked seasonality. Still, the lines do *not* generally disappear (Ferguson *et al.* 1982, but see Horner *et al.* 1999, 299).

As early as 1939, Bryuzgin concluded that "in snakes, like in fishes, in winter, during the period of cessation of nutrition, the bone grows scarcely if at all" (1939, 404). He found lines of arrested growth on the *os transversum* of grass snakes (*Natrix* spp.) to consistently, clearly, and effectively reflect the known number of over-winterings (see also Petter-Rousseau 1953). Examination of his illustrations (see Fig. 7) indicates that a certain amount of skill in interpretation is required. Snakes were also studied by Peabody (1958 and 1961), Castanet (1974) and others, all reporting generally good annual cycles of growth layers. Tropical snakes' patterns are similar to those of temperate snakes, allowing their annuli to be used for ageing.

Lizards have been studied extensively, often with large samples; the simple structure and frequent absence of remodelling make their bones easy to work with. Rock lizards' (*Lacerta*) femurs have bone layering that has proven effective for ageing to within a year or two despite resorption (Castanet and Roche 1981; Smirina 1974), though resorption can confound results (Smirina 1974). What is particularly interesting is that the layers are the same for both parthenogenetic and bisexual *Lacerta* (Arakelyan and Danielyan 2000). The effects of a mild climate on layer formation have also been studied for lizards. Patnaik and Behera (1981) found apparent annual lines on the bones of *Galotes versicolor*, but other researchers have pointed out that the lines are less distinct than those in lizards in temperate climates (Castanet and Gasc 1986; Castanet and Baez 1991). Other lizards and snakes are also reported to have useable annuli (Castanet 1974, 1978, and 1994; El Mouden *et al.* 1997; Buffrénil and Castanet 2000).

Turtles have bone as well as shell growth rings (Mattox 1936). However, resorption often partially destroys the former, and they reflect *size* more directly than *age*. Castanet and Cheylan (1979) provide a correction factor using carapace weight/length, allowing this bone data to serve as a supplement to scute-dating. All these conditions make it of only occasional value to the zooarchaeologist. While reporting his findings in dinosaurs, Horner *et al.* stated that simple counting of lines of arrested growth "now appears to be potentially unreliable" (1999, 302). In general, then, reptiles *do* have growth rings, but a simple reading is not possible, and ageing must be done with caution, taking various factors into account, and even then, in some cases, the results will not be as precise as one would like (Griffin 1962; Suzuki 1963; Enlow 1969, 67–69; Horner *et al.* 1999).

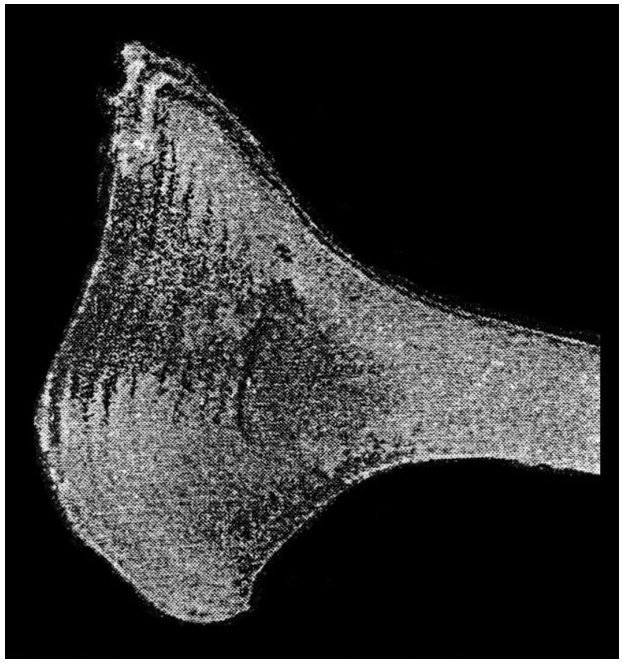


*Fig. 7. Os transversum of a nine year old grass snake (*Natrix natrix*) with incremental lines (From Bryuzgin 1939, 404, fig. 3).*

*Avifauna.* While well-marked layering is sometimes seen in bird bones (e.g. Chinsamy *et al.* 1994), it does not seem to be very promising for age determination in avifauna, especially in light of the considerable resorption that occurs (Hodges 1974). For example, Van Neer *et al.* report that their data on modern chickens "show clearly that there is no relation between the number of endosteal layers and the age of the individuals…" (2002b, 132), verifying their generally negative survey of the usefulness of growth rings for ageing birds. On the other hand, while Lapeña and her colleagues reported poor results in mandibular growth lines from partridges, they did get apparently accurate results from martins' mandibles (Lapeña *et al.* 1993, cited in Van Neer *et al.* 2002b, 128).

*Mammals*. The following survey highlights mammals that are of particular interest due to growth ring quality or special archaeological significance. Most of this material has been gathered or reviewed by the leading authority on mammalian growth rings, G. A. Klevezal (1996). Generally, the locus of choice is the mandible just below the ramus or last molar, though this is not always the case. Additionally, when this site is not available or adequate, other locations on the mandible or on other

bones can sometimes be used. Long bones and ribs are among these other potential bones. Whether vertebrae can be used, as they have been to a certain extent with fish, seems not to have been investigated.

Pinnipeds were among the first mammals for which correlations between bone growth rings and age were developed, and almost all marine mammals have been demonstrated to have bone and/or teeth growth lines. Over three decades ago, Klevezal and Kleinenberg noted that all pinnipeds have readable growth rings but included the caveat that since resorption was a serious problem, many loci have to be sampled (1969, 95). On the other hand, Klevezal has more recently (1996, 157) noted contradictory results. In addition, it seems that after twenty years in males and ten years in females, the mandibular annuli readings can lose their otherwise good readability. In cetacea, the odontoceti have good growth rings, whereas no rings have been reported for the mysticeti (Buffrénil 1982; Klevezal and Kleinenberg 1969, 85, 86).

Few insectivores are long-lived. Shrews and others not living over two years, have readable growth rings indicative of over-winterings (Klevezal and Kleinenberg 1969, 44). Even longer-lived insectivores, specifically, moles and hedgehogs, have good mandibular growth rings coinciding in number with dental annuli (Klevezal 1996, 124–126). Admittedly, these and most other vertebrate species reported have been examined in only small samples and from geographically restricted areas, but the overall pattern has been repeatedly substantiated.

A number of studies on lagomorphs all produced good or very good results of winter-annuli correlations. For example, a study of 57 European rabbits found only two mandibles that did not have the same number of lines and years of age – and these two were actually off by only one month (Henderson and Bowen 1979). The effectiveness of mandible growth rings in ageing lagomorphs is especially encouraging, since the nature of hare and rabbit teeth practically precludes their use in ageing (Klevezal and Kleinenberg 1969, 49; Klevezal 1996, 54, 145, 146, 149). Pika over-winterings get recorded in their annual layers (Klevezal and Kleinenberg 1969, 49).

Rodents, with their peculiar physiologies, e.g. usually ever-growing teeth and a highly efficient calcium supply system, have to be examined for different types of patterns. Marmot mandibles provide accurate growth rings up to 4 to 5 years, but then often stop. Long bones seem to be even less effective than mandible growth-ring ageing. Hamster and souslik growth rings are good up to 3–4 years. Gerbil mandibles are apparently even less reliable than other rodents, one winter being clearly marked but further marks apparently having no chronological meaning. Squirrel radii bones provide better annuli than mandibles or any other tested bones, but additional lines are frequent. Two important and very common rodents have had a number of studies done on them. Mice mandibles have good growth rings, with winter resting lines over 90% effective. On the other hand, rats are controversial. While some studies have found no correlation of growth rings and age, others have reported fairly good results. Interestingly, Klevezal reports that experienced readers of vole growth rings were able to accurately age rat mandibles using the same method. One very important problem distinguishing a single year is identifying "the difference in the formation of annual layers in animals of early and late litters in the same" year due to porosity of bone (Klevezal and Kleinenberg 1969, 79) (rodents: Klevezal 1996, 130–150; 2002. mice: Klevezal 2001).

Bats have very fine bones, with special functions. Possible growth rings are inadequate in number, apparently due to apposition stopping (Klevezal and Kleinenberg 1969: 48). On the other hand, promising results have been suggested in alveolar bone (Schowalter *et al.* 1978 as reported in Klevezal 1996).

Ungulates often provide the bulk of non-human bone at archaeological sites. Thus, it is unfortunate that due to resorption, growth rings are absent from the bones that have so far been examined (including the ubiquitous long bones (Klevezal 1996, 171–177). Compensating for this absence are the effective lines in cementum for some ungulates (see above), and the potential of osteon ageing (see below).

At least smaller carnivores generally exhibit lines of arrested growth in a number of bones, though the extent to which these lines reflect annual cycles is not totally clear, apparently under-reporting years (Klevezal 1996, 96; see also Pascal and Castanet 1978). Klevezal (1996, 156) warns of errors in carnivore bone ageing "due to the high sensitivity and short period of persistence of the record." She also notes a number of the studies, mostly on mustelids, showing better results with cementum. On the other hand, the errors reported (except in some mustelid studies) are more "margins of error" than totally wrong (Klevezal 1996, Table 5). In addition, weasel growth lines were not seen at all in one study (Klebanova and Klevezal 1966) and reported in a study of British weasels to have been egregiously affected by body weight (King 1979). Stoats seem to stop at three growth lines (Klebanova and Klevezal 1966) or are perhaps no good for ageing at all (King 1991, 31). Suggested reasons for the difficulties are remodelling and winter feeding habits (Klevezal 1996, 96), the latter being supported by the fact that hibernating animals produced clear winter lines of arrested growth. Larger carnivores, like large mammals in general, have had few reported studies, annual rings supposedly not formed or observable in many of them.

While Klevezal does not mention studies done on primates, she does in passing state that "apposition of bone tissue in a human rib normally takes place at [i.e. through?] the age of 60–69" (1996, 18).

*Conclusion*

Numerous hard tissues exhibit growth rings on various

scales, the most common being annual and the next, daily. At least for most vertebrates, the best of these rings seem to be on various dental tissues. Bones (and other materials not covered in this paper) are also fairly effective recorders of age. Because of factors involving specific species behaviour, environmental variables, and differing bone composition, growth and resorption; a simple equation of major lines with years of age or over-winterings and/or minor lines with months or days is not possible. Instead, individual species and macro-environments must be considered in order to accurately read the lines. Fortunately, a lot of work has been done so that, with adequate training, the archaeozoologist can age remains of scores of species using growth rings. On the other hand, even in well-researched taxa, there are a number of problems that might be encountered. In addition to the limitations listed at the end of the section on dental growth rings, there are the following similar restrictions on bone: the growth rings are often absent for whatever reason; climatic conditions can mask lines or conceivably induce extra ones. Resorption is a problem on most long bones of most large and fast-growing animals; missing, multiple, and unclear lines can lead to minor or even major errors in counts. Finally, of course, the bones or parts of bones that are needed can also be missing or in a bad state. Where these problems are present, other histological approaches might be effective.

Still, it has been noted that there are a number of species where growth rings have already been shown to be effective ageing devices. Some of the rings occur in bones and teeth that are sometimes found in great abundance at archaeological or paleontological sites. From Peabody (1961) through Klevezal (1996), researchers have noted the impact of the environment on the width of growth bands. If a large enough sample is present, it stands to reason that it could be used to set up a local or even regional floating *dating* sequence, analogous to early dendrochronologies. Not only could such a sequence be used for dating, but specimens that have broken records could be matched to the master curve and thus be aged. This idea might seem far-fetched, but it seems, at least theoretically, possible, and striving for it might refine our tools.

### *Osteons*

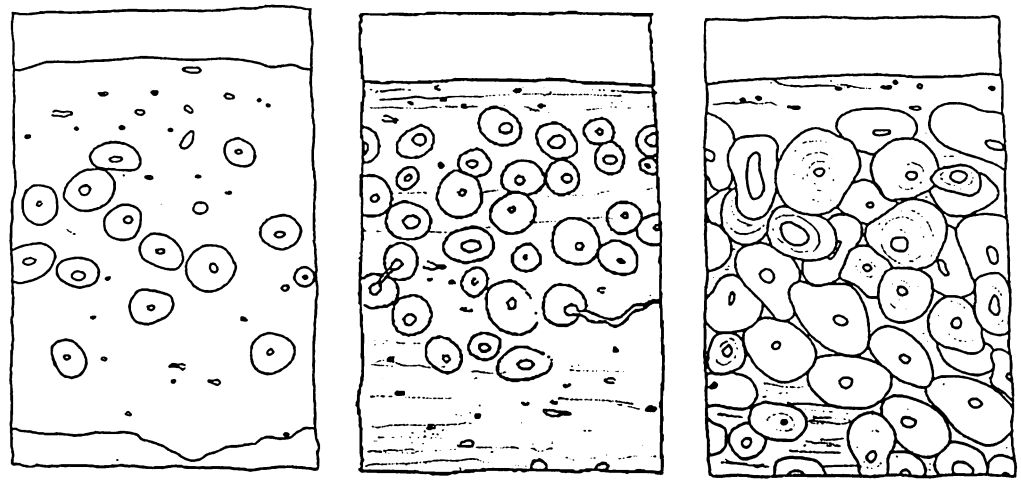
As already mentioned, growth rings in bone and teeth can be problematic for ageing. Therefore it makes sense to look at other histological indicators. So far, this means osteons and their environments. Over sixty years ago, Amprino and Bairati (1936) noted specific changes in bone histology of animals as they grow older, and in their encyclopedic study of vertebrate osteohistology, Amprino and Godina (1947) made cogent generalized observations about the trends in bone fine structure as it grows older as did Filogamo (1946) and Enlow (Enlow and Brown 1956–58; Enlow 1963). While the specific changes vary with bone and taxon, there is a general pattern of three stages: 1) growth, 2) growth and change (remodelling), and 3) regressive change (remodelling). Schmidt *et al.* (1981) applied these stages to human bone, but they have been shown to be applicable to many or most species, especially longer-lived ones. More specifically, bone modeling begins in infancy with no secondary osteons, followed by secondary osteons that are usually large and irregular as remodelling begins. Small canals form in "youth," followed by smaller osteons and increased fragments in adulthood. Finally larger, often unclosed osteons form with increased numbers of smaller interstitial (i.e. fragmentary) lamellae, and large resorption lacunae in individuals that reach an old age ("senility"). While Amprino's observations form the basis of the qualitative method for ageing *Homo sapiens*, no concerted effort has been made to produce equivalent refinements in more than a few other species even though informal use is sometimes made of this knowledge (e.g. Lind 1994). Likewise, the quantitative methods that have been developed for humans have had almost no testing in other species.

*Humans*. Efforts at using osteon characteristics to determine age-at-death have concentrated on humans. The approaches can be divided into two classes: quantitative and qualitative. The former approaches, developed in the English-speaking world and also used in many other countries, attempt to count and measure any number of variables. These include size, frequency, and relative area of secondary and primary osteons, interstitial lamellae, and canal diameters in pre-specified locations on most long bones, ribs, and, less commonly, the mandible and skull. These measurements are then matched with the values for known ages-at-death to come up with precise correlations and a statistical range. For a survey of most of the numerous quantitative methods as well as a general discussion of this class of ageing, see Robling and Stout 2000. The variables usually used are non-linear in their distribution over age. Thus, simple single-variable correlations or linear regressions, though giving values that for some samples are within three or so years, are inherently limited. On the bones, samples from midshaft are generally advised. Because osteon distribution is not symmetrical around the bone and counting is time-consuming, and since collection administrators do not always allow removal of a complete chunk of bone, sampling procedures have been developed or, perhaps, "evolved." Thus, it is generally recommended that four or more samples be taken, located equidistant around the shaft, extending from periosteal to endosteal bone. The most effective (i.e. accurate and precise) factor combinations, as well as the best bones and loci cannot really be specified, since the techniques have generally only been "tested" on the same material – even the same data – from which they were generated. In addition, different

ages appear to vary in factor effectiveness. There are a number of technical difficulties with these quantitative approaches. Some of the problems are ameliorated by the qualitative method explained below. In counting or measuring osteons, what constitutes an osteon can be a problem. While this seems like a resolvable problem when one reads the procedures, a look at actual slides reveals that identifying osteons can be quite difficult. Even with image-processing software, there are difficulties and ambiguities. A few of the studies have examined intra- and inter-observer reliability, but a recent article (Lynnerup *et al.* 1998) has reported discouraging statistics in this area. Even though semi-automatic software has sped up the counting and measuring, it has not resolved the accuracy issues. Another significant problem deals with loci. In trying to be objective and consistent in using a limited sample, researchers can be confronted with unacceptable material (i.e. bone that has taphonomical, physiological, or pathological anomalies), and the suitability of the bone may not be known until after the sampling. Bone is often not expendable, and a further sample might not be available. A final difficulty is familiar to zooarchaeologists: the bone one is presented with is not necessarily what one would consider ideal. For the histologist, the problem is not the fragmentary nature, but bones or bone regions for which no good correlation between histology and age exists. Fortunately, however, central parts of long-bone shafts are the elements most likely to survive archaeologically and resist fungal and other modifications; these are the preferred objects for histological ageing. A last and final impediment is that the condition of the macro-states can belie a totally different degree of preservation on the cellular level. On the other hand, the moderate independence of the state of the two levels means that we can switch from one to the other on occasion to get more information.

The qualitative method for ageing, developed in Göttingen and practiced in Germany and neighboring countries, takes a holistic approach: A number of factors are weighed to get an age range. While this might at first seem subjective and requiring extensive training, ageing this way can in fact be learned quite rapidly. While I know of no formal studies testing for consistency, in practice people with just a few hours training generally produce consistent ageings, a condition maintained over years. While a non-lab description of the method is not enough to make one a practitioner, it can give a good idea as long as one follows up with hands-on work. Perhaps the key to the qualitative method is its flexibility in finding an appropriate area of the bone to use. The general location, i.e. midshaft on long bones, is the same as for the quantitative method, but the worker is not forced to use exact loci that might be damaged or hard to read. Furthermore, by using an *impressionistic* approach, this method is quick and maximizes the human ability to recognize patterns and tendencies while taking into account anomalies. Fig. 8 shows the six major age categories in their idealized forms. These stages can, in turn, be subdivided to reflect transitional states, in effect give ageings often both closer and surer than those produced by the quantitative methods. A recent discussion of the latter notes that they "all use linear regression equations, which are notoriously limited…. Confidence intervals are neither small nor equivalent but expand as the regression line moves away from the mean" (Meindl and Russell 1998, 387; no mention is made of qualitative studies). The qualitative method has been found effective with small, burned bone fragments as well (Hummel and Schutkowski 1993). Recently, "super osteons," giant canal systems that occur away from midshaft, have been examined and reported to increase fivefold from 20 years of age to 80 (Bell *et al.* 2001a). Using super osteons thus appears to be a potential additional ageing index. A modest number of other animals have been examined for osteon or general histological change over age. The following is a sample of some of the more interesting and relevant cases.

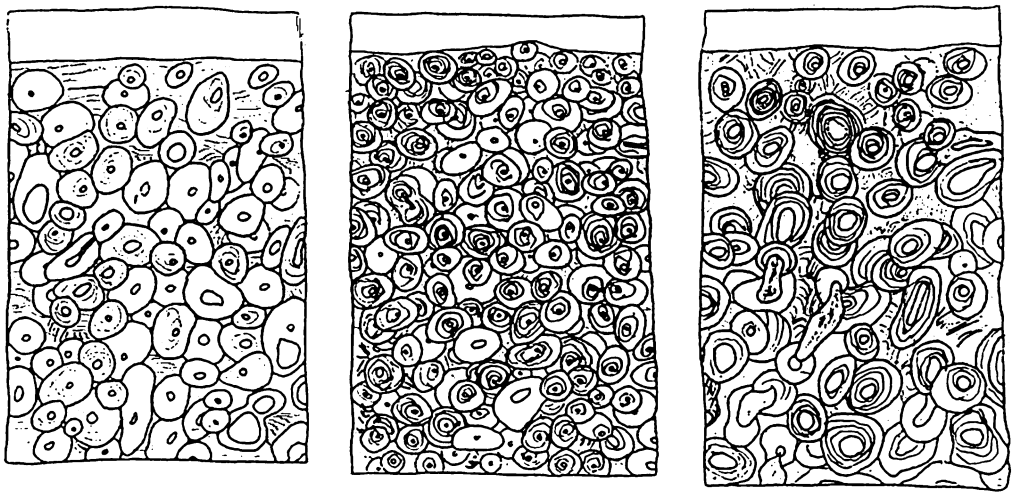
*Primates.* Osteohistological studies on primates of known age have produced modest to promising results for predicting age using factors involving osteons. The bone turnover in female rhesus macaques (*Macaca mulatta*) is clearly different for growing, adult, and menopausal individuals, according to Colman et al. (1999), though no specific mention of osteons is made in their paper. Przybeck (1985) studied the osteohistology of the ribs of 15 macaques (sex not indicated), ranging from 4 to 31 years of age. Results of his limited sample suggest that intact osteon density and osteon fragment density can produce a good qualitative scale. For the youngest animals, intact osteons are more diagnostic, while fragments appear to be more useful in mature individuals. Havill (2004) recently reported an increase in femoral osteon density with age in her sample of 75 free-roaming rhesus monkeys. A statistically significant, relatively linear correlation showed age accounting for 23% of the variation in density. Bowden et al. (1979) found only extremely weak correlations between age and histological factors for pigtail macaques (*Macaca fascicularis*), with femoral osteon density showing a tendency to decrease with age, though anomalous individuals clouded the statistics (Table 27–4 on p. 341). What *does* come across in these results is that "variation in degree of remodelling […] clearly increased in the older age groups […]" (342–343). The authors also pointed out an easily noted increase in the number of partially mineralized osteons and irregular borders of osteons (p. 343), indicating that a qualitative scale might work. More recently, Burr (1992, 187; see also Burr *et al.* 1989) found in a study of femurs of 54 individuals that "[v]ariation in bone microstructure occurs independent of gender, age, and body weight in growing macaques." On the other hand, he does note that the rate of osteon accumulation in *growing* macaques (but not in most other primates) seems to be stable and



infans 1
*predominantly lamellar bone; some isolated primary osteons, resorption lacunae*

infans 2
*increase in primary osteons and resorption lacunae; LAGs or pseudo-LAGs possible*

juvenis
*large osteons: can be aligned, irregular in shape, with small Haversian canals; general lamellae*



adultas (20–40 yr.)
*small osteons, percent that are secondary increases; irregular distribution; general lamellae; some lamellae as osteon frags.*

maturitas (40–60 yr.)
*very small, regular, round osteons, closely packed; no general lamallae; more osteon frags.*

senilis (60+ yr.)
*larger, irregularly shaped osteons with large Haversian canals; large resorption lacunae; many osteon frags.*

*Fig. 8. Qualitative osteology for ageing human bone: generalized drawings of six primary stages of long bones in cross section (modified from Hummel 2001, 32).*

that osteon population density is greater in adults (Burr 1992, 185). Lees and Ramsey (1999) noted differences in the histology of the iliac bone of young (3–4 yrs.), mature (10–15 yrs.), and old (22–24 yrs.?) cynomolgus monkeys, saying that the results were similar to those for rhesus monkeys. Thus, at least a distinction between growing and adult macaques seems to be possible. Schaffler and Burr (1984, 192–193) reported fifty percent more (14.6 vs. 9.7) osteons per millimeter in the femur of an adult spider monkey (*Ateles fusciceps*) than in that of a subadult (*A. paniscus*). On the other hand, there was no real difference (7.7 vs. 7.4) in the values for an adult and a subadult *Pan troglodytes* (Schaffler and Burr 1984, Table 1 on p.192). Mulhern and Ubelaker (2003), on the other hand, found moderate age-related changes in the microstructure of juvenile chimpanzees (N=12) and significant

changes for the one 35-year-old. For juveniles, age "predicts 9–44% of the variation in chimp femoral microstructural variables" (2003, 130). The clearest indicator was the number of non-Haversian canals, which decreased with age. Unfortunately, no indication of sex is given in this study. The differences between mature and old were dramatic.

Since primate osteohistological studies tend to focus on locomotion and on contrasts with humans for use in medical research, some bones that might be useful for ageing have not gotten adequate attention to determine their feasibility.

*Carnivores.* Examining images of mandibles from Arctic fox, sable and mink in Klevezal and Kleinenberg (1969), one can see that an increase in the density of osteons takes place as these animals age. Stanek (1970) specifically observed the rate of osteon growth in young dogs.

*Ungulates.* In hog, peccary, cow, ox, and goat, there are well-organized plexiform structures in the periosteal bone. "In the formation of this bone, lamination of vascular canals occurs […] connected with short, radial canals" (Enlow and Brown 1958, 204). Metatarsals of a young and an old rhinoceros (Amprino and Godina 1947, Figs. 90 and 91) had the following suggestive differences: secondary osteons of various sizes as well as fragments are already present in the young animal but become the only kind in the adult, where they are even more disorganized in the cortical core. By comparing the osteons in the mandibular diastema of young and old wild Asiatic asses, we can see that they become more compact and appear to have cement lines and to become less layered (Klevezal and Kleinenberg 1969, 101 [Fig. 61]). The investigators note specifically: "in the young animal, the main bulk of the buccal [cheek] wall consists of reticular bone tissue and bone plates divided by many canals giving passage to blood vessels; on the exterior we observed a very narrow periosteal band without adhesion lines [...]. The lingual wall was completely osteonized. In the old specimen, both the buccal and lingual walls were fully osteonized" (Klevezal and Kleinenberg 1969, 102). In the axis deer, there is rapid resorption. In the illustrations in Klevezal and Kleinenberg (1969, 107, Fig. 66), the difference between the two mandibles (six years and eight years) is so great that I am inclined to think that it reflects a special case. However, if it is not idiosyncratic, this rapidity of change would make for easy ageing. Jane Ruddle (1997) explicitly tested the applicability of the quantitative approach as performed on humans, to roe deer. Using a sample of mandible rami from 30 bucks and 42 does, up to 14 years old, she found that the total and average non-Haversian canal counts correlated highly with age, the latter having an average inaccuracy of 2.5 years and an average bias of -0.04 years. This is not as good as tooth-wear ageing, but of value where dentition is absent, she concluded. This success with a moderately long-lived and archaeologically significant animal is very encouraging.

*Rodents.* An early quantitative examination of rat histological change showed that the pattern in these short-lived mammals is close to that of humans. In fact, these are the most dramatic results of osteon ageing. Using a control laboratory sample of 35 rats from 2 to 120 days of age, Singh and Gunberg (1971) found very good agreement for femur, tibia, and mandible. Readings on the last of the bones provided an accuracy of ±1.5 days for 67% and ±3 days for 95% of the population's true ages using a simple regression based on increasing number of secondary osteons, lamellae and "Haversian canal diameter and non-Haversian canals" (250). Thus, specific histological changes in rats are in agreement with the known general osteoid maturing pattern of more osteons forming with ever-more constricting rings – but for *this* species, to an extent, that is outstanding. A cautionary note: since the rats were from a controlled, single-sex sample, variation is almost certainly less than what occurs in nature.

*Lagomorphs*. Rabbits have a histological make-up different from that of rodents. "The vascular pattern […] is longitudinal, and the structural arrangement and formation of the primary osteone is not comparable [to that of rodents]. In the development of new primary bone, the deposition of periosteal lamellar layers alternates with vascular strata. Each primary canal is surrounded by one, two, or three rings of osteocytes forming a Haversian-like structure. These primary vessels may extend across the greater portion of the compacta without secondary intervention, or areas of dense Haversian reconstruction may occur. The ribs and skull bones are largely Haversian structure, and well-developed secondary osteones appear in several generations" (Enlow and Brown 1958, 211). A quantitative study (Korkmaz *et al.* 1996) found a good ($r>0.9$) correlation between increase in number of osteons and age in the long bones (femur, tibia, humerus, ulna, and even radius) of *Lepus capensis.* Also increasing with age were what they called "interval lamellas" (presumably interstitial lamellae), while non-Haversian canals decreased with age.

*Sea mammals.* Klevezal and Kleinenberg (1969) report for the mid-mandible of the sei whale (*Balaenoptera borealis*), that "macrocircular laminas [are] osteocized, in small [i.e. young] specimens less so than in large ones" (85).

*Marsupials.* Amprino and Godina (1947, Figs. 54 and 60) show that primary bone, with small vascules, is replaced with the spread of secondary osteons, but not to the periosteal surface. They also note that there is a development of extreme disorder and that fragments help separate islands of primary bone.

*Avifauna*. Except for aspects related to the need for lightweight bones, the osteohistology of birds is similar to that of mammals (Hodges 1974). Unfortunately, wild birds seem not to have been studied for correlations between age and changes in general bone histology. Domesticated chickens have been fairly well studied. In their early pre- and post-hatching development, their Haversian canals, overall histological structure mineralization, and cortical width are outstanding age markers, differing from day to day, but only up to two to three weeks post-hatching (Caplan 1988; Williams 2000). In a recent survey of the literature on the histology of birds, Rensberger and Watabe (2000) stated that "[l]amellar bone is scarce in birds and coelurosaurs, and where it does occur, it is poorly organized" (621).

*Reptiles.* Enlow (1969) describes a variety of general developmental changes in reptile histology (59–66) roughly like that of mammals, including one peculiar to crocodilians and turtles that further studies could likely stratify into age groups. Certainly, there are clear differences between neonatal, young, and mature that can already be designated. In fact, for some dinosaurs and other early reptiles this has already been studied (Chinsamy 1995; Horner *et al.* 2000; Ray and Chinsamy 2004). Here are some specific modern reptiles: Slider turtles have a clear pattern of cellular development, with males and females fairly similar but with a lag in female bone and some variations depending on location on the bones. Specifically, in males of the length of 65–100 mm, by the time of attaining the maximum length the "vessels within the cortices were primarily longitudinally arranged with some radiating communicating canals of Volkmann" (Suzuki 1963, 357). This is followed by a transition "to an outer primary longitudinal vascular bone with an inner endosteal Haversian bone" (357). The Nile monitor lizard's tibia goes through a decrease in the number of vascules, which also become radial in arrangement and larger (Amprino and Godina 1947, Figs. 5–7). It is possible that there is an increase in order, contrary to what happens in vessels (osteons) in many other animals. While most of the emphasis on dinosaur histology has been on lines of arrested growth, a number the researchers have also noted and discussed differences in osteons and other microscopic bone structures when comparing younger and older individuals, e.g. Erickson and Tumanova (1995, 2000), who in one species found numerous stages of vascular patterns, from longitudinal through reticular to radial, rather than the usual Haversian systems of other dinosaurs (Reid 1997b).

*Amphibians.* The bone microstructures of very young and adult frogs differ. For example, in the young bullfrog the bone "is nonvascular, but subsequent peripheral deposition results in simple vascular bone tissue" (Enlow and Brown 1958, 214). The potential here for using general histological structure to at least develop age *groups* seems to be quite good.

*Conclusion*

There are certain general patterns that pertain to the changes in osteonal bone with few exceptions regardless of the bone and species, as long as that bone type is present in a species. The extent and rate of these changes vary markedly. What is needed is a series of studies of local samples of various species with known ages and sexes to develop fine-scaled charts of the specific nature and rate of these changes.

### *Conclusion*

Up until now, histological research on ageing (especially for bones) has concentrated on the so-called second order, the scale of the growth lines, osteons and lamellae themselves. The tools have been simple microscopes to examine two-dimensional images of cross-sections. Histology of non-lamellar bone has been all but ignored when it comes to attempting age determination. This is now changing, or at least being augmented by new tools that can image non-invasively or on finer scales, with automated programs and ones that produce three-dimensional images.

## Sexing with Osteons

There has been little direct work on sex determination using osteons or other histological landmarks. This paucity is likely due to the fact that there are easier and presumably more effective methods in osteology. What work *has* been done is characteristically indirect, with the researchers usually looking at sex-related factors or simply controlling for sex. Indirect studies can be put into five groups: *empirical studies*, *mechanical stress*, *disturbances*, *female functions*, and *the third sex*. Some early osteonic studies disregarded sex, and others claimed that it made no difference. Later studies showed that sex *does* statistically make a difference, even in *Homo sapiens*, a species with only moderate sexual dimorphism. Thus, the more careful quantitative studies now *do* separate by sex, so as to get cleaner results.

### *Empirical Studies*

An innovative study (Smitmans *et al.* 2000) using SAM to examine the acoustic impedance of lamellar osteon ensembles of a sample of human material covering a very wide age range also compared differences in sex. While impedance generally increased over age with no particular difference between the sexes, there was reversal of this trend in the oldest males. The decline is small and gradual, but for either a large collection or an older range group, SAM offers some promise for sexing well-aged animals that live to the advanced age category. However, work has only been reported on one species so far. Another, clearer difference was the one-third higher rate

of young osteons in women than in men (Bell *et al.* 2001a, b). In a work that is difficult to obtain, Egeli (1976) reported on the differences in osteon sizes in men and women. While both boys and girls exhibit a continuous decrease in osteoid surface extent as they grow older (from 34% before 6 yrs. to 17% by 23), the rates vary by sex (Glorieux *et al.* 2000). Given the tight ageing, this discrepancy might fairly be used to infer the probable sex in young humans. The same study also found differences in osteoblast surface extent between the two sexes.

Burr (1992, 187) found bone microstructure of no predictive value for determining the sex of growing macaques. On the other hand, Havill (2004) reported that osteons in mature males are larger than those in mature females. While she points out that the size difference can be explained by bone (or body) size, for archaeological samples it can be used as an indicator of sex.

In both raccoon dogs and badgers, a *number* of differences have been recorded between the sexes, including osteon short diameters and osteon density (Hidaka *et al.* 1998). Osteon diameters in humans have also been reported as being greater in adult males than in women (Brockstedt *et al.* 1993), suggesting that this factor could discriminate in a number of species. Klevezal (2001) reported an accuracy rate of sexing *Apodemus* mice mandibles histologically at over 80%.

Suzuki (1963) noted that male slider turtles have a thick cortical wall and massive Haversian canals in the endosteal region, in contrast to females. This species also offers a good example of a sexual difference in age of microstructural change, as mentioned in the ageing section above, that can provide information for sex determination.

### *Mechanical Stress*

Wolff's Law states, somewhat hyperbolically, that the bone responds to loci of stress. In both bone build-up associated with muscle attachment and use, and in impact stress, the changes are actually activated on the microscopic, chemical level, with the living bone bringing up reinforcements to provide improved infrastructure. It is almost as if the body *knows* what it will need and plans for it, whereas *how* it "knows" and exactly how the mobilization takes place is not understood by scientists. As we know, within a given population, human males tend to develop larger muscles and more robust and denser bones; some corresponding differences are seen in the osteohistology. The same can be hypothesized for other sexually dimorphic species (or reverse, for species with more robust females). Histomorphologically, many of the distinctions based on robustness in macromorphology are observable less clearly, but with the same exceptions and overlap.

### *Disturbances*

The most common disturbances are injuries and diseases. Histological analysis of disturbances associated with a particular sex can, like macromorphological studies, suggest the sex from bones of the individual from the microscopic changes if they are present. Beyond the influences of disease and injury are the long-term behavioural ones. In humankind, we have the tennis elbow (which does *not* show the expected histological change) or the well-known grain-grinding activity often associated with women in Neolithic cultures (I do not know of any studies on the histology here, as opposed to those on the macromorphology). But there are also behavioural differences in other species as well: consider the differences in hunting styles of the lioness and her male counterpart or the differential use in many cultures of cows vs. bulls and stallions vs. mares, or primate and marsupial carrying of young. This issue, unfortunately, has hardly been examined.

### *Female Functions*

It is not surprising that osteohistologists, in general, focus on females. The physiological effect of hormonal changes and rhythms are more obvious than in men, though the extent to which the influences are direct is still far from clear. Thus, menarche, menstruation, pregnancy, parturition, lactation/nursing, weaning, and menopause, each have been associated with changes in resorption as seen in histological studies in various species. Physiologically, these associations are not surprising: each of these phenomena makes a significant and different demand on the body's resources, especially the calcium and iron. Unfortunately for sexing purposes, many of these changes are transitory. For other changes, some permanent, see the study of parturition-lactation zone in the cementum of souslik teeth in Trunova *et al.* (1999), as well as Klevezal and Sukhovskaya (1995) on mice teeth, Rosenberg and Simmons (1980) on rabbits and pregnancy, and Kagerer and Grupe (2001) on a correlation between bright lines and pregnancy/parturition in women's cementum**.**

### *Menarche/Sexual Maturity*

In slider turtles, the females' osseous changes take place at older ages than do those of the males. Thus, if the age can be determined – e.g. by scute annuli – the sex should be histologically determinable in individuals whose development of ≥65 mm carpal length has not yet plateaued. For example, male turtles with carpal lengths of 65–100 mm have a much heavier layer of endosteal Haversian canals than do females of the same age (Suzuki 1963).

In humans, sex differences for changes in bone microstructure have been reported on two occasions. The first

was the age of onset of resorption patterns in the cortex of bones of teens, with peripheral resorption coming earlier in females. This earlier resorption occurs around menarche, either due to the accompanying change in physiological stress or associated with the general pattern of earlier maturation we know in girls. Glorieux *et al.* (2000, 108) suggest that histological sex differences in girls "might be the result of differences in the timing of puberty." If a subject can be age-dated to within a year or so and the age falls within the early-to-mid-teens, this fact can be used to sex the individual. Usually if we have enough data to age an individual that accurately, we have enough gross morphology or DNA to sex with greater probability of accuracy than histomorphologically, so the point might seem moot. However, this procedure might find better application in other species, ones that exhibit or suggest appreciably different onsets of sexual maturity, or something of the kind, between the sexes.

*Reproduction (pregnancy, parturition, lactation)*

Chamberlain and Forbes (2001, in press; see also Forbes 1994) found a clear difference in distribution of osteon size in femurs of beef cattle (male and female) and of dairy cattle (obviously female). The dairy cattle osteon size distribution was statistically identical to that of cattle from a Roman site in England from around AD 100. A diagnostic pattern seems to exist, though it does not have to be sex-related *per se*. Unfortunately, whether it is due to behaviour (extensive/intensive care), diet, breed, dairying/lactation/milking, or whether it is a reflection of age, is not clear since the dairy cattle were all much older than the beef cattle (2 yrs.). Since remodelling and differences in osteon size and density are related to at least both lactation and age, this study has opened a door to sexing techniques (Saddha Kuippers, pers. comm.). In any case, there is an osteonal difference between young beef cattle of either sex and older milch cows. Whether it is due to the hormones or the treatment (or extraneous factors), it is possible that this study will lead to identifying sex if we know that in a given culture *milked* cows were the only cattle kept to an older age.

Since lactation puts a strain on the calcium supply, it is to be expected that in most species (unlike rats, which are efficient enough calcium producers to handle this strain with ease), there will be a histological effect from nursing. Transient increases in intracortical bone remodelling reflects the drain on the mother's calcium resources. Lactation in beagles, for example, strongly remodelled the bone, with a significantly different make-up in osteon composition and resorption spaces (Vajda *et al.* 1999, 1441–1443). These dogs, however, were from a highly controlled lab population, so the results are probably clearer than would occur in nature. It should also be pointed out that this and almost all female function studies use other females and not males as controls. The fact that the change is transitory also reduces the diagnostic value of lactation changes. Vajda also notes studies that have shown a correlation between lactation and changes in *cancellous* bone in sheep, pigs, monkeys, and other animals, "[h]istomorphometry revealing that the lactation-induced decrease in bone mass is associated with a marked increase in cancellous bone remodelling as reported in dogs… and rats…" (Vadja *et al.* 1999, 1439).

Another study (Ott *et al.* 1999) looked at macaques. Osteoclast density increased during pregnancy and was still present three months after weaning. These results are quite promising, though the variability was very large. An archaeological report by Trivers and Armelagos (1977) suggested that a hypermineralized ring directly around the Haversian canal or slightly farther out decreases with lactation in humans. Thus, a small variety of effects on osteons has been reported associated with reproduction and lactation. To what extent the effects of demands on the mother's system, mostly for calcium, repeat across species (or even samples) is not known, since the variables measured differ from study to study.

*Menopause*

Resorption of medullary bone in middle age begins earlier in women than in men. The onset in women might be linked to menopause. One could hypothesize a similar difference in age of changed resorption pattern for other long-lived mammals, such as horses, deer, dogs, cats, wolves, monkeys, apes, and elephants. In humans, ageing on undocumented individuals is too inexact to make this slight shift of use in sexing individuals. However, statistically the difference is enough to calculate a population sexual distribution given a large enough *maturens* sample. In any case, bone mineral density and turn-over are well documented in menopausal females, including in monkeys (e.g. Champ *et al.* 1996; Colman *et al.* 1999; Cerroni *et al.* 2000) as well as humans, even though the work is generally not histological. On the other hand, dental growth rings seem to be accurate enough to enable the use of this shift for sexing (my speculation); likewise for species where bone growth rings are present and complete enough to allow for close ageing. Late mature individuals and ones with greater resorption than "expected" for their closely determined age could thus be sexed for any taxa also exhibiting the sex difference in age of middle-age resorption onset.

## *The Third Sex*

Certain domesticated animals are castrated in a number of cultures. The surgery can be undertaken for a number of purposes: to improve docility, to control populations, to fatten animals for meat, or to control singing voice (in humans). It stands to reason that this massive modification of the hormonal system would leave its mark on the microscopic structure of hard tissue.

Castration has been shown to affect the development of the histology of antlers, generally producing a juvenile

appearance, with a lack of secondary osteons (Kierdorf *et al.* 1995, 38–39, 41; Bubenik 1990, 281–283).

Castration also affects the structure of bone, generally reducing the bone density (Winks and Felts 1980). In rats, the accompanying structural changes include a sparcity of trabeculae and an obvious increase in resorption cavities in femurs. However, the mandibles were unaffected in all aspects studied. The difference seems to appear more in load-bearing bones. Another contributing factor affecting histological changes is the age at which castration is performed. Strangely, animals castrated at one year but *not* those operated on at twenty-three days exhibited change in bone structure! Since (early) castration in larger male animals can apparently alter the morphology of some bones (e.g. bull metacarpals; the pelvis) to the point of shifting them into the range for females (Chaplin 1971, 103–104; Deborah Ruscillo, pers. comm.), it is possible that histological studies could also show an analogous shift for them.

### *Summary*

Thus, a number of differences occur either incidentally or inherently in the microscopic bone structures of the sexes. However, no special effort has been made to compare them across the taxonomic landscape. While space restrictions have essentially limited my discussion on sex to osteons, in fact, bone and tooth annuli also reflect many of the same forces. The interested reader is directed to Laws (1953), Spencer and Uhler (1955, 75–82), Klevezal and Kleinenberg (1966, 116), Carlson (1990, 543), Klevezal (1996, *passim*), and Klevezal (2001). When only small fragments are present, macromorphology is often stymied. Furthermore, the best bones for morphological and histological sexing are not the same. DNA sexing is still expensive and not always effective, e.g. in some cases of burning, where osteons can be quite robust. In truth, though, it seems there will be only some occasional cases, such as dog or human cremations with teeth remains and bone splinters, where histological sexing will prevail.

## Conclusion

We can envisage a continuum from the macroscopic/morphological over the histological to the chemical and molecular. There is a rough corollary with this ever finer, ever smaller focus: the less visible the objects of study, the longer it takes and the more complicated and expensive it is to get results. Osteonal and other histological studies have several advantages, perhaps foremost of which is the generally robust character of the osteons: small, broken pieces of burned bone are adequate material (Grupe and Herrmann 1983/84; Hummel and Schutkowski 1986; Cattaneo *et al.* 1999); and it is the strong shafts of long bones, along with some cranial material, the most persistent of bones, that are best suited to osteon analysis. An additional useful feature is that once the thin-sections have been prepared for ageing, say, no further preparation is necessary for tests of stress, disease, and sex. In fact, these tests often should be undertaken together to get the most accurate results. Additionally, the thin-sections are small and generally long-lived. To a certain extent, the osteohistological methods developed to date are complementary to each other. This is often true in terms of species and bones as well as the obvious (though small) difference in location on the bones. On the other hand, some of the taphonomic depredations affecting one affect the other.

Obviously, both grosser and finer methods also have certain advantages as well. The decision as to what particular tool or tools to use depends on the nature of the remains and the questions to be asked (as well as funds and time), and should not be determined *just* by the availability of an expert or even the lack of knowledge of the *existence* of alternative methods and techniques. In some cases, a combination of methods can bring better results than individual techniques used separately. Furthermore, there is still enough mystery in animal histology that such studies can profit from such cooperation. As David Browman put it in another context in *Early Native Americans* (1980, preface), we need to "attempt to breed hybrid vigor by mixing a variety of approaches and directions together." While a fair amount is known about osteons, especially in taxa determination (e.g. Foote 1913; Mátyás 1927; Amprino and Godina 1947; Enlow and Brown 1956–58), ageing of *Homo sapiens* (Pfeiffer 1992; Robling and Stout 2000), a bit about aspects of domestication (Richardson *et al.* 1961; Lasota-Moskalewska and Moskalewski 1982; Gilbert 1989; Forbes 1994; Chamberlain and Forbes 2001, in press), and certain aspects of stress (Burger *et al.* 2001; Skedros 2001) and disease (Pfeiffer 2000); more focus needs to be put on the usual suspects – cows, pigs, goats, horses, dogs – as well as deer, birds, and other common game and commensal animals, especially in terms of ageing.

*Acknowledgments*

I would like to thank Deborah Ruscillo for care in organizing the ICAZ ageing and sexing session and her support and help throughout the session and editing this volume. I also thank Jaco Weinstock and Elaine Turner for their critical reading of an earlier version of my paper. Bryan Gordon, Wim Van Neer, and Darius Batulevicius provided helpful advice. Andrew Chamberlain graciously allowed me to use a number of definitions from the web site of University of Sheffield's Department of Anthropology. For generously granting me the free use of illustrations, I gladly thank the editors of the *Turkish Journal of Zoology* as well as Gary Rosenberg and the Springer-Verlag. I acknowledge the generous travel funds to attend ICAZ 2002 granted by the Institute for Aegean Prehistory.

## Glossary

**N.B.**: The definitions given here are aimed at providing simple and understandable descriptions to help in following the literature rather than authoritative definitions (see Gordon 1993). For the latter, see, e.g. Carter 1990; Francillon-Viellot *et al.* 1990; Parfitt *et al.* 1987; and *Report of the Workshop* 1980, as well as standard science and medical dictionaries. Italicized terms are defined elsewhere in the glossary.
Definitions marked with an asterisk (*) are from Sheffield, no date:
**http://www.shef.ac.uk/uni/academic/A-C/ap/thin_sections/glossary.html** (with possible orthographic changes), used with kind permission.

**adhesion line** older term for recording structure or cement line.
**ageing** determining of the age-at-death or, for living individuals, the amount of time since (or before) birth. Bones, teeth, etc. lost during life are aged to age-at-time-of-loss, i.e. to the age at which the item rather than the individual died. *Ageing* is to be distinguished from "dating," which refers to length of time before the present or before or after some external date.
**alkaline phosphatase** a phosphate-releasing enzyme secreted by *osteoblasts* that calcifies the matrix.
**anastomosed** (integrally) joined.
**annulus** (*pl*. **annuli**) a ring-like structure or part, e.g. on trees, shells, teeth, and in bones (cf. *growth rings*). It is sometimes also understood as a year's ring. This can be confusing, since there is nothing innate in their being the same. Some authors (e.g. McKinley and Burke 2001) use the term to refer only to regions of reduced centrifugal growth with few cells, and contrast *annuli* with *LAG*s (no cell, opaquer in polarized light), and both with *growth zone.* Erickson (1997) simply describes *annuli* as thin layers of avascular bone fibres.
**apatite** calcium phosphate, the main mineral of bone.
**BMD** bone mineral density.
**BMU** (**bone maintenance unit / basic multicelluar unit**) the package of various bone cells that carries out remodelling.
**bone modelling** "the acquisition and transformation of overall bone form and shapes by differential variation of local growth rates" (Francillon-Viellot *et al.* 1990).
**bone remodelling** see *remodelling.*
**bone structural unit** the tiny packet of new bone formed in *resorption* and found in *Howship's lacuna.*
**bone turnover** change in chemical and/or structural composition of bone.
**BSU** *bone structural unit.*
**canaliculi** (*sg*. **canaliculus**) fine channels through bone that form an *anastomosing* network between the osteocyte lacunae. In living bone the canaliculi are occupied by the cytoplasmic processes of the *osteocytes*.* They run perpendicular to the *Haversian canals*.
**cancellous bone** spongy bone containing interconnecting cavities.
**cement**(**um**) a cellular mineralized fibrous organic material that is laid down on the exterior of a tooth's root, accreting in bands, the most exterior of which are the most recent. These bands are effective *ageing* indicators.
**cement line** *reversal line*. *Cement line* is usually reserved for a reversal line occurring in an *osteon*. On the other hand, Francillon-Viellot *et al.* (1990, 505) and Klevezal 1996, 18) define *cement lines* as including both *resorption lines* and *resting lines*.
**circumferential lamellae** (**circumferential lamellar bone**) sheets of *lamellar bone* lying parallel to the *periosteal* and *endosteal* bone surfaces.* Bone "composed of evenly spaced bands, or *lamellae*, that run parallel to each other around the outer part of the cortex. It appears as birefringent sheets in polarized light and can be distinguished by its long, parallel fibers. [It…] is a prominent feature of childhood" (Kerley 1965, 151).
**collagen** a [tough] fibrous protein that constitutes the principal organic fraction of bone. * There are various types of collagen, but all in the form of a triple helix. Collagen comprises over 85% of the mineral content of bone.
**compact bone** (**compacta**) bone which has few "open" spaces; it includes most external surfaces. "The differentiated compacta of the bones of mammals usually consists of a mesiosteal zone, and also an outer and inner layer of generative plates" (Klevezal and Kleinenberg 1969, 9). It makes up about 4/5 of bone mass in humans. Cp. *cancellous bone*.
**concentric lamellae** *lamellae* in *osteons*: surrounding the *Haversian canal.*
**cortical bone** dense bone, or all dense bone with a network of parallel *collagen*; essentially, a synonym for *compact bone.*
**demineralization** laboratory removal of mineral (primarily calcium) by treating with acid.
**dentin(e)** acellular (and generally mineralized) organic substance which accretes in the tooth's pulp cavity, advancing inward in layers. These resulting bands are effective indicators of *ageing*.
**diaphysis** shaft of a long bone.
**drifting osteon** a type of secondary osteon found in some young animals; the osteon moves sideways by osteoclasts eating away the matrix on one side of a recently created osteon, while osteoblasts fill in on the other side (Robling and Stout 1999).
**endosteal** referring to the outer surface of a bone; the opposite of *periosteal.*
**endosteal bone** the internal surface of *cortical bone*, adjacent to the *medullary cavity.**
**endosteum** the one-celled layer which lines the *medullary* (inner) *cavity* within the long bones. It is osteogenic.
**epiphysis** secondary ossification center found at the neck of long bones.
**fibro-lamellar compact bone** "a complex of 1) woven or fibrous, cancellous matrix of *periosteal* origin, and 2) a *lamellar* matrix, centripetally deposited, forming the *primary osteons* which ultimately fill the space originally empty in the woven *periosteal* matrix. Vascularization is plentiful, although variable, and evidence of growth cycles is generally rare" (Carter 1990).
**fragmentary osteon(e)s** (**osteon(e) fragments**) partial *osteons*, the remains of osteons broken down by *osteoclasts* building new (*secondary*) *osteons.*
**growth layer** a *growth zone* plus an associated *annulus* or *LAG* (McKinley and Burke 2001).
**growth layer group** a repeated pattern of incremental *growth layers* (Hillson 1986, 224), considered to represent one of a number of temporal units, especially a year.

**growth mark** "any variation in growth recorded at the morphological or histological levels in any sclerified tissue…" (Francillon-Viellot *et al.* 1990, 507), and occurring as a *growth zone, annulus,* or a *rest line*. *Incremental growth layer.*

**growth ring** any ring or line indicating a period of growth; "refers to cases in which periosteal bone of Gross's zonal type (1934, 742, as *zonare Periostknochen*) is divided into tree-ring like zones by the cyclical development of major resting lines… or bands of dense bone termed annuli…" (Reid 1990, 21). Synonyms and near-synonyms include: *incremental line*, winter incremental line, winter resting line, daily layer, zone of hibernation, *parturition-lactation zone*, dental growth mark, incremental growth line, circadian increment, polish line, bone layers, line of arrested growth, *annulus*, *adhesion line*, and *recording structure*. Use has not yet become standardized, so that the same term can have different meanings from author to author and a different term for the same concept will be found from article to article. Where the author is dealing with the physiology itself, s/he will usually explain her or his use adequately for one to follow the article.

**growth zone** a layer of bone *not* characterized by slow or stopped growth. It is translucent in *polarized light* (McKinley and Burke 2001).

**Haversian bone** "Bone which has been largely remodelled into *secondary osteons*" (O'Connor 2000, 6).

**Haversian canal** one of the minute canals which traverse many dense bones in a wandering manner, generally following the major axis of the bone. They convey nutrients (via blood vessels, nerves, and lymph vessels) to bone through their subordinate adjuncts including *osteocytes*. A *Haversian canal* is the center of a given *osteon* (*Haversian system*).

**Haversian lamellae** *lamellae* (sheets of dense bone) around *Haversian canals* which were formed during *osteon* formation and accrete concentrically inward.

**Haversian system** *osteon.*

**histology** the study of the microscopic structure of biological tissue and function; loosely, such structures themselves.

**Howship's lacunae** the surface depressions on bone surface left by *osteoclasts* where bone *resorption* occurs, located between the *osteoclast* and the bone resorption surface.

**hydroxyapatite** a complex crystal of calcium phosphate crystal, Ca10 (P04)6(OH)2, that makes up practically all of bone mineral and makes it hard and stiff.

**incremental growth layers** "distinct layers parallel with the formative surface of a hard tissue (*dentine*, bone, *cement* and their subtypes) which contrast with adjacent layers" (Hillson 1986, 224). According to Hillson, this terminology is standardized for marine mammals.

**incremental line (IL)** a general term for *incremental growth layer* or *recording structure,* and often *growth layers* or and *annuli*. However, its use is sometimes restricted to just lines reflecting stoppage or slowing of growth.

**inner circumferential lamellae** *lamellae* found adjacent to the *endosteum*, i.e. near the *medullary cavity.*

**interstitial lamellae** (**interstitial lamellar bone**) remnants of older *Haversian lamellae* and possibly of *inner* and/or *outer circumferential lamellae.*

**lacuna** See *osteocyte lacuna*.

**LAG** *line of arrested growth.*

**lamella** (*pl.* **lamellae**) any of the thin plates of fibre, found 1) bundled centripetally around *Haversian canals (Haversian lamellae)*, 2) occurring as fragments of the previous type of lamellae in *compact bone* (*interstitial lamellae*), 3) added centrifugally (*periosteal lamellar bone* or *outer circumferential lamellae*), or 4) added centripetally *(inner lamellar bone* or *inner circumferential lamellae*) to dense bone.

**lamellar bone** dense bone with fine *collagen* fibres organized into sheets of a few microns thickness (*lamellae*), within which the fibres are parallel in orientation.*

**laminae** "bone with zonal '*growth rings'*[…;] bone between successive vascular networks (*sensu* Foote 1916, 11)…[;] "bone between successive 'bright lines' or successive layers of *periosteal* woven bone if 'bright lines' are lacking [*sensu* Currey 1960…]" (Reid 1990, 23, 24).

**laminar bone** (**laminar Haversian bone**) bone in which the osteons appear to be lying in layers. A classic case is found in numerous dinosaur bones. According to Reid (1990, 23), Foote included both zonal and *fibro-lamellar* tissues, causing confusion in subsequent work.

**laminar fibro-lamellar bone** Reid (1990, 23) notes various uses: *laminar bone* (Currey and Reid), laminar and plexiform fibro-lamellar bone (de Ricqles), *plexiform bone* (Enlow), *laminare Periostknochen* (Gross).

**line of arrested growth** (**LAG**) a line on a bone, tooth, etc. representing a band of growth, in which the growth slowed, characteristically causing denser deposits. The slowing can be caused by stress or slowed metabolism. The centrifugal growth (in *periosteal LAG*s) is said to stop. Thus, Erickson (1997, 4) describes it as an avascular layer thinner than and having fewer fibres than an *annulus* has. A LAG is a particular kind of *growth ring*.

**line of resorption** a usually distinct, sometimes wavy, line indicating the outermost margin of (extensive) bone remodelling, i.e. the boundary between the *mesiosteal* and *periosteal* zones. It is presumably always axial to any growth rings that (still) exist.

**marginal zone** in an *osteon*, the outermost band, bounded by the *cement* (*reversal*) *line.*

**medullary cavity** the central tube within the bone which houses the marrow, responsible for generation of blood cells.

**mesiosteal zone** the intermediary part of *cortical (compact) bone*. "The mesiosteal zone forms as a result of the reconstruction of the primary bone tissue" (Klevezal and Kleinenberg 1969, 9). The osseous zone of *cortical bone*.

**metaphysis** the site of ossification, between the *diaphysis* and *epiphysis.*

**microtome** an automated sawing machine that cuts off fine slices. It is very easy to operate but quite expensive.

**mineralized** having had minerals deposited as a crystalline or amorphous mass in a pre-existing matrix (bone or *cartilage*).

**non-Haversian canal** primary vascular channels "formed at the time the surrounding lamellar bone was formed, […representing] areas of unremodelled bone" (Kerley 1965, 151–2). Essentially the same as *primary osteon(e).*

**osteoblasts** secretory cells responsible for building new bone (*lamellae*).

**osteoclasts** large, multinucleated bone cells that tear down old bone by secreting an acid.

**osteocytes** bone cells which have lost their ability to produce bone material and are trapped within their matrix. These are the remnants of the *osteoblasts* which form bone tissue as the bone is developing, are located within/between the *lamellae*, with *canaliculi* radiating toward the central *Haversian canal* and other *osteocytes* in the *osteon*.

**osteocyte lacuna** [usually referred to as simply **lacuna**, *pl.* **lacunae**] a round, ovoid or lenticular space within which an *osteocyte* resides in living bone tissue.*

**osteohistology** the *histology* of bone; loosely, the histology of animal hard tissue or at least of bone and teeth.

**osteoid** precalcified bone matrix composed mostly of *collagen.*

**osteon(e)** (**Haversian system**) a structural unit of bone consisting of a central (Haversian) channel with blood and lymph vessels, nerves, and connective tissue surrounded by concentric cylindrical layers of *lamellar bone* of osteocytes in an *apatite* matrix. *Volkmann's canals* radiate laterally from the *Haversian canal*, allowing distribution of the blood, etc. on a finer scale. See *secondary osteon* and *primary osteon.*

**Osteon(e) Population Density** (**OPD**) "[(osteon number + osteon fragment number)/mm$^2$]: the number of *secondary osteons* with intact *Haversian canals*, plus the number of *osteon fragments*/square mm averaged for all observed cortical fields" (Havill 2004).

**osteon(e) fragments** *fragmentary osteon(e)s.*

**outer circumferential lamellae** (**outer lamellae**) (*sg.* **lamella**) the thin layers of bone laid down as the bone is formed. They lie just below the *periosteum* and form the outer surface of the *compact bone* tissue.

**parturition-lactation zone** an area of bone with a distinctive pattern coinciding with parturition and lactation.

**Percent Osteonal Bone** "[(osteonal area/cortical area) × 100]: proportion of the observed cortex occupied by secondary osteons with intact Haversian canals" (Havill 2004).

**permineralized** fossils having their original pore space infilled with minerals.

**periosteal** referring to the outer surface of a bone; the opposite of *endosteal.*

**periosteal bone** the external surface of *cortical bone*: "the outer generative plates [...] deposited as a result of apposition activity" (Klevezal and Kleinenberg 1969,9).

**periosteum** vascular membrane covering the surface of a bone's shaft and having osteogenic potential. Osteologists sometimes also use the term to refer to the surface of the bone itself.

**petrification** the process or condition of original material of an organism being replaced with minerals after death.

**plexiform bone** bone in which the *lamellae* are grouped into layers separated by well-developed vascular channels or by bands of *osteons.**

**polarized light** light waves whose plane of vibration is confined to a particular orientation.* This is often an effective way of viewing bone sections under a microscope.

**primary osteon(e)** usually a small *osteon* that is not bounded by a reversal line but instead is surrounded by conformable layers of *interstitial* or *circumferential lamellar bone.** Essentially the same as *non-Haverian canal.*

**recording structure** persistent layers of hard tissue that reflect response to changes in the physiological parameters of an organism as it grows or undergoes environmental impact. (Klevezal 1996, 3). It includes both *lines of arrested growth* and *annuli*. Replacing the designation *adhesion line*, this term is a near synonym to *growth ring* or *incremental growth layer.*

**remodelling** the body's *resorption* and reconstruction of bone (or other dense tissue) through biochemical activity, especially by *osteoclasts* and *osteoblasts*, resulting in a new or modified shape.

**remodelling line** *resorption line.*

**resorption** the biochemical reworking of bone through incorporating old structures into new ones. This is primarily done by *osteoclasts*. See Parfitt 1993.

**resorption lacuna** (*pl.* **resorption lacunae**) volume in *compact bone* which has been resorbed without subsequent replacement by *Haversian systems.*

**resorption line** a wavy band about 1–2 μ across indicating the edge of *resorption* either within an *osteon* or mediosteally, where it marks the inner limit of still-existing centrifugally growing *growth rings*. It is essentially synonymous with *reversal line* and is sometimes also called a *remodelling line* or *cement line* (q.v.).

**resting line (rest line)** a line, characterized by a smooth border, reflecting a pause in centripetal or centrifugal growth, i.e. a *LAG* (Francillon-Viellot *et al.* 1990, 505).

**reticular bone** a type of *fibro-lamellar bone* in which primary osteons in *lamellar bone* are obliquely oriented and connected to each other.

**reversal line** narrow zone of hypermineralisation that demarcates the boundary between the termination point of *bone resorption* and the initiation point of new bone formation. Sometimes referred to as a *cement line*.*

**ruffled border** edge of osteoclasts facing the *Howship's lacunae* and wavy in shape.

**sealing zone** that area that to which an *osteoclast* attaches and in which it creates a *Howship's lacuna.*

**SAM** scanning auditory microscope.

**SCN** *suprachiasmatic nucleus*.

**secondary osteon(e)** **a**n osteon that has developed in a *resorption* space within pre-existing bone tissue; distinguished by its interception of pre-existing *lamellae* and by its hypermineralised border (*reversal line*).*

**SEM** scanning electron microscope.

**sexing** determining of the sex of an individual to whom the tissue under consideration belonged.

**skeletochronology** (**sclerochronology**) "the study of [faunal] mineralized tissue for the purpose of determining intervals of time with reference to the organism being studied" (McKinley and Burke 2001, 34). The "study of recording structures apparent in mineralized vertebrate tissues" (Pike-Tay 1999, 297). (Note that these two definitions are not identical, the former allowing for other histological *ageing* methods such as those based on osteons and the latter not unless *recording structures* be redefined. It should also be noted that *skeletochronology* is usually restricted to vertebrates, and *sclerochronology* includes – often exclusively – invertebrates).

**super-osteon** remodelling cluster with a central canal having a diameter greater than 385 microns (Bell *et al.* 2001a, b).

**suprachiasmatic nucleus** (SCN) part of the brain that regulates circadian rhythms.

**trabecular bone** cancellous bone containing interconnecting cavities having "a precise three-dimensional spatial arrangement which reflects mechanical forces acting on the bone" (Francillon-Viellot *et al.* 1990, 491).

**vascular canal** small tube within bone that provides a pathway for blood, nerve, and lymph lines. Varieties include the central canals of *primary* and *secondary osteons*, as well as simple primary vascular canals without surrounding *lamellae*.

**Volkmann's Canals** vascular channels running perpendicular to the *periosteal* and *endosteal* surfaces, connecting the vessels in the *Haversian canals* and (in some cases) connecting with vessels in the *periosteum* and the *medullary cavity.**

**woven bone** highly vascularised bone tissue with coarse,

undulating, interwoven and randomly orientated *collagen* fibre bundles and randomly distributed *osteocyte lacunae*; found in embryonic and fetal bone, fracture callus, and in the *medullary* bone of egg-laying birds.*

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*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 40–61*

# 3. A Method to Estimate the Ages at Death of Red Deer (*Cervus elaphus*) and Roe Deer (*Capreolus capreolus*) from Developing Mandibular Dentition and its Application to Mesolithic NW Europe

*Richard J. Carter*

*Radiographic studies have been made of red and roe deer molariform dentition from the early Mesolithic sites of Star Carr, Thatcham, Mullerup, Holmegaard, and the late Mesolithic sites of Tågerup, Segebro, Ageröd, Skateholm, Bökeberg, Tybrind Vig, Ertebølle and Ringkloster. Mandibles of known-age from various modern European populations have also been radiographed, thereby generating two comparative reference data sets, one archaeological and one modern. The ages at death of Mesolithic juvenile red and roe deer have been assessed from the radiographs of developing molariform dentition. The results provide new evidence that red and roe deer were killed during the winter at some early Mesolithic sites and support for existing summer indicators at others. At two inland late Mesolithic sites, red deer were killed during the summer and early autumn whilst at the coastal sites, a mixture of seasonal evidence has been found. New models of settlement are proposed in which there was less seasonal mobility amongst both early and late Mesolithic groups. The degree of seasonal movement between early Mesolithic inland and coastal sites is considered and previous models in which there is a reliance on the postulated coastal sites are questioned. Permanent base camp status is tentatively proposed for some inland late Mesolithic sites and their role within a predominantly coastal-based economy has been reassessed.*

## Introduction

New seasonal evidence has been obtained from the early and late Mesolithic sites of Star Carr (Carter 1997, 1998), Thatcham (Carter 2001a), Holmegaard I, IV, V, Mullerup Syd, Tybrind Vig and Ringkloster (Carter 2001b), Tågerup, Segebro, Skateholm I, Bökeberg III, Ageröd V (Carter in press) and Ertebølle (Carter 2001c). These results were obtained using a technique that assesses age at death of dentally immature fallow deer (*Dama dama*) and red deer (*Cervus elaphus*) from radiographs of developing mandibular premolars and molars (Brown and Chapman 1991a, 1991b). The author applied this scheme to age juvenile red and roe deer (*Capreolus capreolus*) from the sites. The selected sites are drawn from the Maglemose, Kongemose and Ertebølle culture periods and both inland and coastal sites are represented. The chronology and location of these sites is shown in Figs 1 and 2. Knowing the age at which red and roe deer were killed provides good evidence of when humans were present at the sites.

The ageing scheme will be summarised, but the reader is referred to the aforementioned papers for more detailed descriptions of methodology and individual site results. The intention of this paper is to examine existing settlement models for the Northwest European Mesolithic and, where relevant, propose revisions based on the new results. It is acknowledged that investigating seasonality of an individual procurement activity, such as killing deer, does not constitute an attempt to establish seasonality of site occupation. However, this paper will attempt to synthesis these new results with existing seasonal evidence and, where appropriate, propose new models of settlement for the NW European early and late Mesolithic.

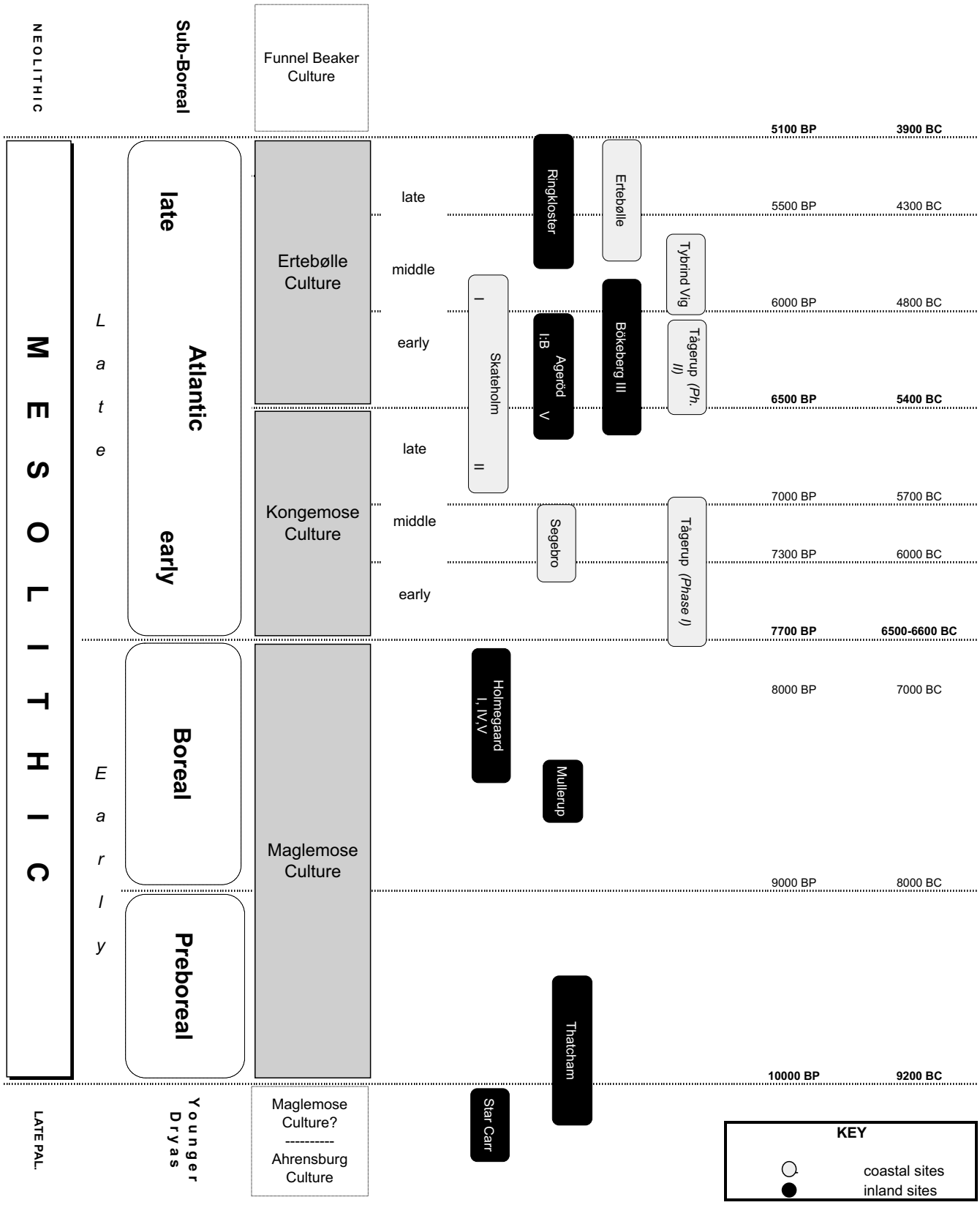


*Fig. 1. Chronological scheme of the NW European Mesolithic and the sites under investigation.*

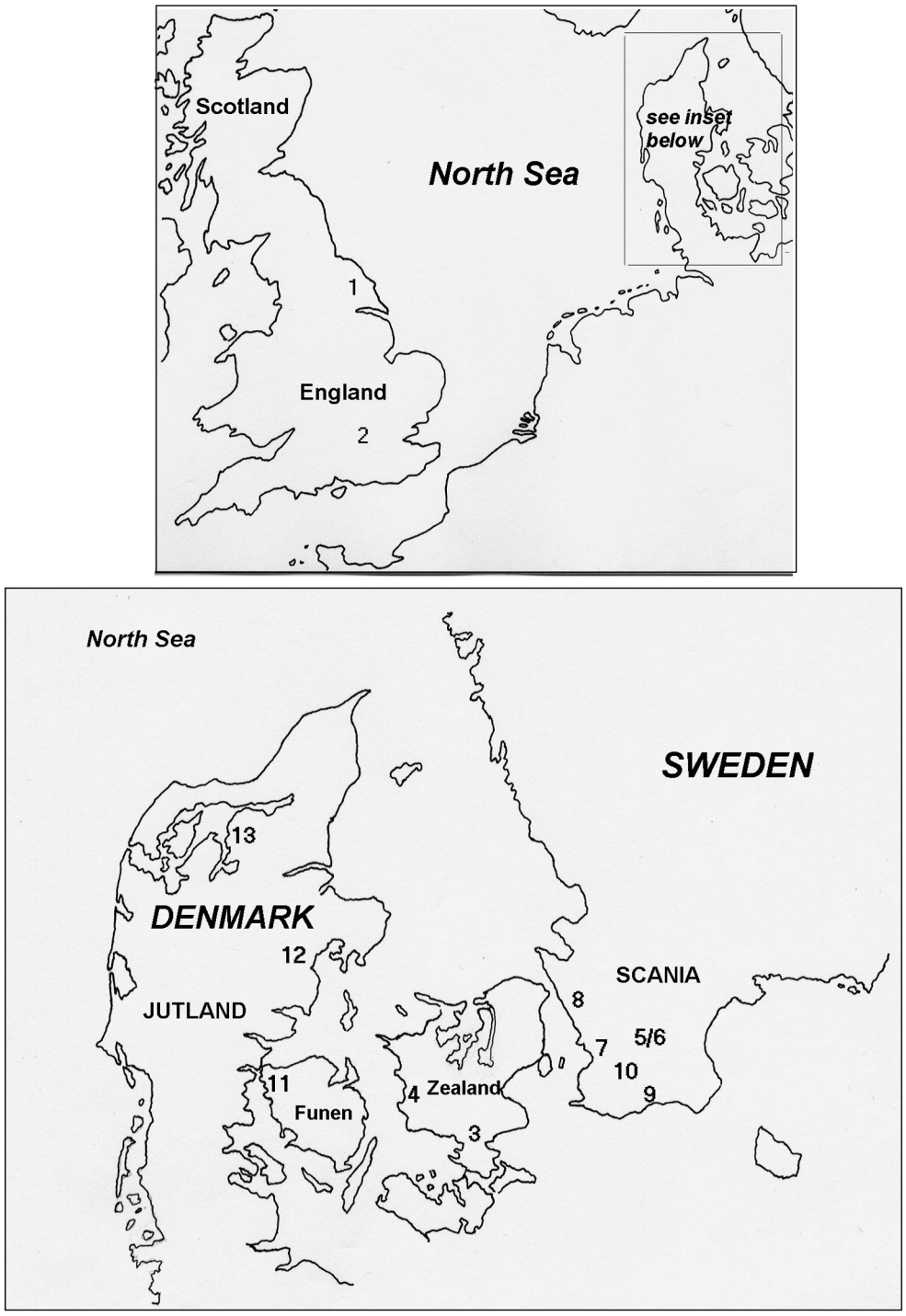


*Fig. 2. Area of study and location of selected sites. (Early Mesolithic: 1. Star Carr, 2. Thatcham, 3, Holmegaard I/IV/V, 4. Mullerup Syd. Late Mesolithic: 5/6. Ageröd I:B/V, 7. Tågerup, 8. Segebro, 9. Skateholm I, 10. Bökeberg III, 11. Tybrind Vig, 12 Ringkloster, 13. Ertebølle).*

**Site seasonality and settlement patterns**

Current seasonality assessments at all 14 early and late Mesolithic sites are represented schematically in Figs 3 and 4. These estimations have been thoroughly reviewed in the author's research thesis (Carter 2001c). For more detailed explanations, the reader is referred to the publications listed in the aforementioned figures for each site. Traditional models of settlement for the NW European Mesolithic will also be described in this section.

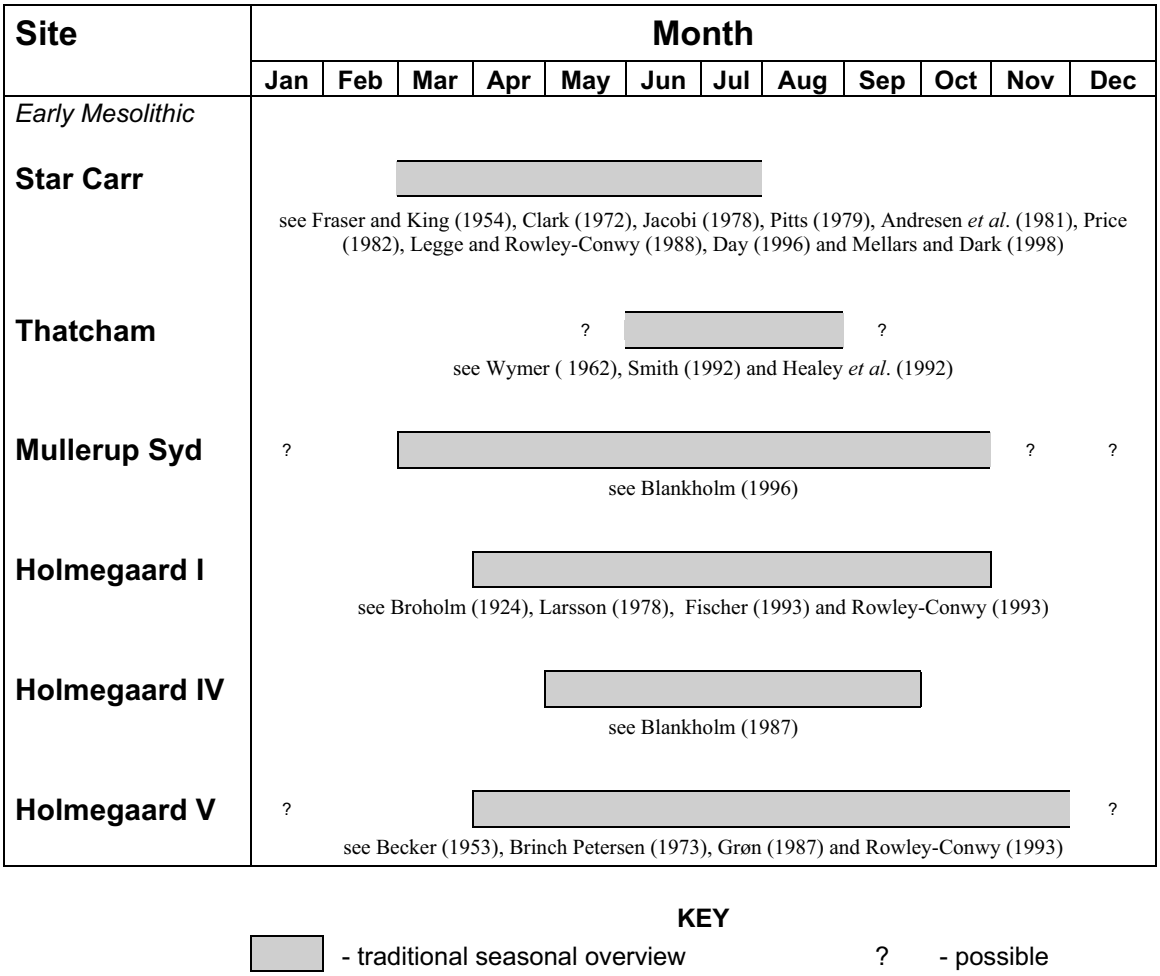


*Fig. 3. Traditional seasonal assessments for the early Mesolithic sites.*

***The Early Mesolithic***

Models of early Mesolithic settlement invariably rely on an assumption that people adopted a highly seasonal pattern of mobility which involved residential moves between different sites (c.f. Brinch Petersen 1973; Price 1985; Smith 1992; Rowley-Conwy 1993; Blankholm 1996; Erikson 1996). It is argued that remaining for any length of time in an area ran the risk of over exploitation of important plant and animal species. Residential mobility incorporating inland and coastal locations ensured any scheduling of resources had the widest possible base.

Blankholm (1987, 1996) proposed a Maglemosian settlement model of summer base camps situated beside inland swamps or lakes where a wide range of activities took place. This proposed short-term occupation of Preboreal and Boreal inland sites is endorsed by Rowley-Conwy (1993). In a study of Danish Maglemosian lake-side settlements, Rowley-Conwy concludes that there is no evidence of winter occupation and that they were 'summer sites'. The function of these sites is unknown, but, based on a study of skeletal element frequency, he believes they were not hunting camps. The possibility that they were base camps is not discounted. It is also suggested that during the winter these sites were abandoned with the occupants aggregating at larger camps possibly located in now submerged river valleys. In contrast Larsson (1978) has proposed that two distinct inland and coastal-based groups may have existed which had contact through social relations and the exchange of goods. Summers were spent beside bodies of water, whether the sea or inland lakes, and winters slightly away from the coast or lake edges. The absence of winter evidence at the early Mesolithic sites can be clearly seen in Fig. 3.

The influence of seasonal factors on economic activities and settlement patterns may have been over-played in the early Mesolithic. In a statement for debate, Lewthwaite and Rowley-Conwy (1980) challenge the classic nomadic hunter-gatherer image cultivated in Mesolithic studies. They suggest that cultures, which had succeeded in making a stable adaptation to their new

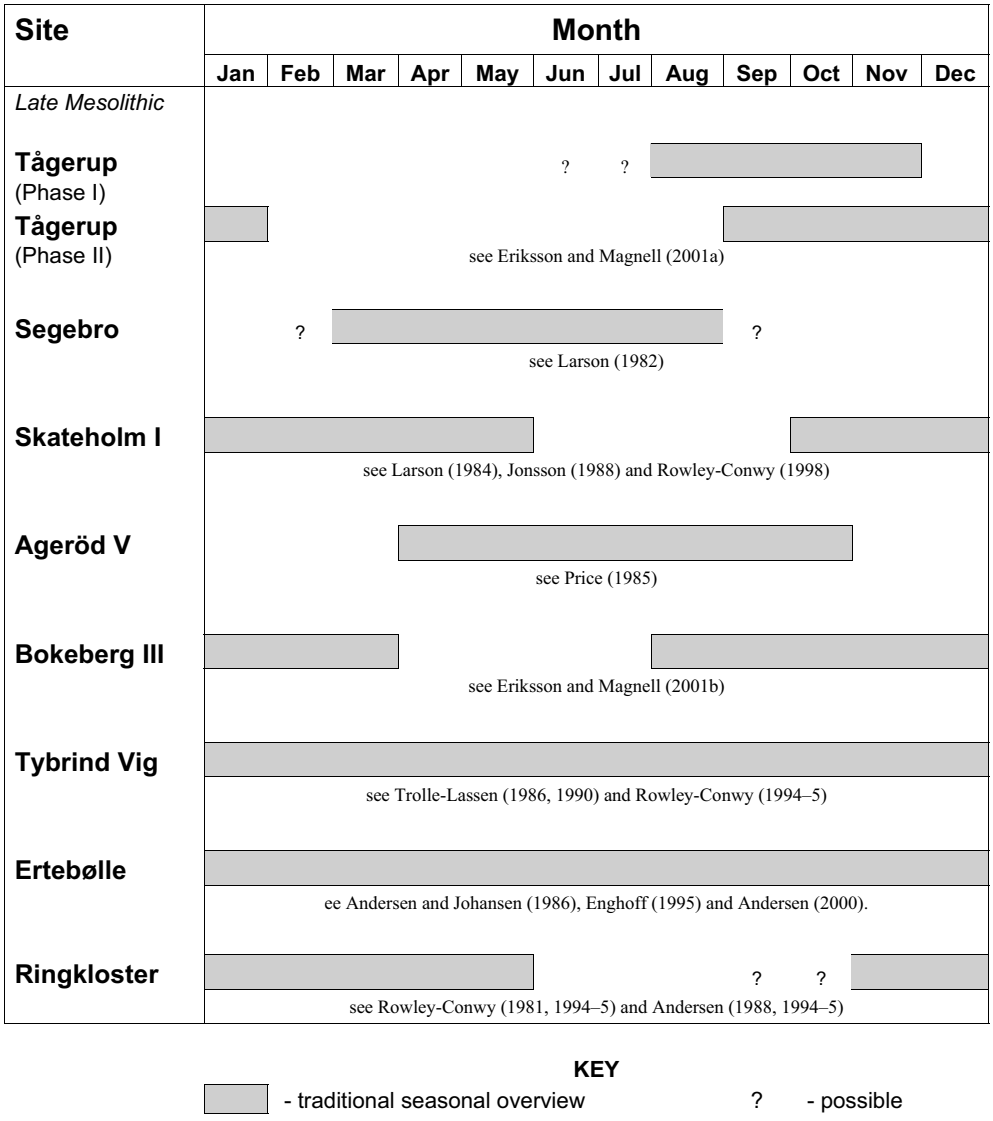


*Fig. 4. Traditional seasonal assessments for the late Mesolithic sites.*

environment, had done so by exploiting its inherent natural abundance. These communities were settled, sedentary and of a reasonable size often located at the coast or in extremely favourable ecological niches. Jacobi (1987) proposed that if the late winter and spring 'resource gap' can be closed then residence patterns can be collapsed into one location rather then spread throughout the landscape. The idea that Maglemosians may have been more sedentary than mobile is not new (Woodman 1985a), and has recently received some support (Day 1996; Mellars and Dark 1998).

### *The Late Mesolithic*

The differential use of coastal and inland resources at various times of the year has been proposed by many authors (c.f. Larsson 1983; Rowley-Conwy 1983; Andersen 1994–5), but the nature of this dependence has been frustrated by a lack of seasonal evidence. A radial and logistic settlement pattern for the Danish Ertebølle period has been proposed by Rowley-Conwy (1999), based on sedentary occupation of the large shell midden sites (c.f. Paludan-Müller 1978; Rowley-Conwy 1983; Andersen and Johansen 1986). These coastal settlements have been described by Andersen (1993) as more densely clustered and extensive than inland sites and having a continuity and stability of occupation. According to Rowley-Conwy (1993) they were maintained by 'temporary special purpose extraction camps' located at favourable locations on islands, at the coast or inland. These highly seasonal camps were occupied only for a short time and sited in order to take advantage of specific resources, not available at or near the parent settlement (c.f. Andersen 1979; Andersen and Johansen 1986;

| Site | Red Deer | Roe Deer | Location |
|---|---|---|---|
| Star Carr | 20 | 13 | Natural History Museum |
| Thatcham | 6 | ~ | " |
| Holmegaard I (1922) | 9 | 3 | Zoological Museum, Univ. of Copenhagen |
| Holmegaard I (1923) | 4 | 1 | " |
| Holmegaard IV | 1 | 3 | " |
| Holmegaard V | 1 | ~ | " |
| Mullerup Syd | ~ | 10 | " |
| Ringkloster | 14 | 1 | " |
| Ertebølle | 4 | 2 | Moesgård Museum, Univ. of Arhüs |
| Tybrind Vig | 17 | ~ | " |
| Ageröd V | ~ | 3 | Univ. of Lund, Sweden |
| Skateholm I | ~ | 1 | " |
| Bökeberg III | 5 | ~ | " |
| Segebro | 4 | ~ | " |
| Tågerup* | 1 | 7 | Riksantikvarieämbetet, Lund, Sweden |

* many single teeth

*Fig. 5. Number and location of specimens from the Mesolithic sites.*

Rowley-Conwy, 1994–5). It is argued that the inland sites were fully integrated into a pattern of settlement and subsistence which saw regular logistical mobility between quite different environments at all times of the year (Rowley-Conwy 1993). Simmons (1996) has proposed a similar model of settlement for the uplands of northern Britain. This involves permanent occupation of coastal sites but with a temporary repositioning of the entire group inland during the autumn months.

A radically different model of late Mesolithic settlement has been proposed in which two distinct coastal and inland-based settlement patterns exist (Larsson 1980; Price 1993). Larsson (1980) thinks it is possible that population pressures resulted in coastal and inland groups occupying permanent camps located at or near river estuaries and lakes respectively. The inland groups were a minimum of 30 km from the sea, but may have seasonally exploited the numerous small fishing locations scattered along the coastline. Andersen (1994–5) has described these separate groups as 'forest hunters' and 'coastal fishermen'. A key feature of this model is the proposal that some Mesolithic groups occupied inland sites during the colder months of the year. Logistic mobility and the need for short-term, possibly seasonal, camps to procure specific resources are common to all the models. The problem is distinguishing between these special purpose camps and the more permanently occupied parent settlement.

The archaeological study of Mesolithic settlement systems is complex (Rowley-Conwy 1987a), but can be approached through an understanding of site function. One of the principal aims of this paper is to achieve this through an increased knowledge of site seasonality. Before looking at the results and any revision of these models, the method used will be briefly described.

## Materials and Method

### *Modern and archaeological specimens*

Assessment of age at death of archaeological specimens of red and roe deer from tooth development relies on the acquisition of modern known age or known kill date specimens for comparative purposes. Roe deer samples from populations in Scotland, England, Denmark, France, Poland and Switzerland have been secured (n=122). Red deer samples originate from Exmoor & Quantocks, Cumbria, Scotland, Poland, and Brown and Chapman's

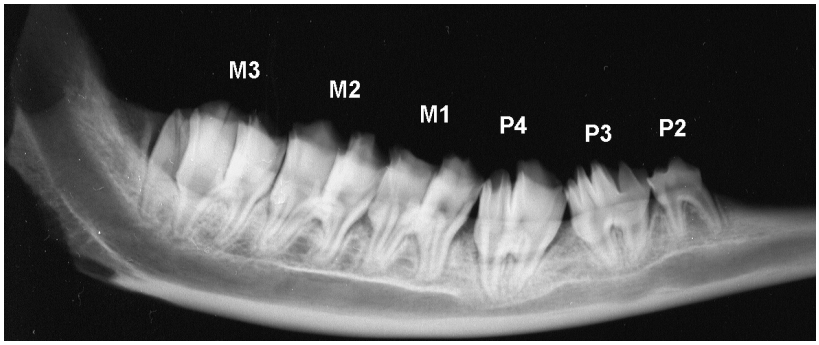


*Fig. 6. Radiograph of a right-sided mandible (horizontal ramus) from a dentally mature Roe deer showing molariform dentition.*

| Stage & Score | | Description |
|---|---|---|
| Decid. | Perm. | |
| (7) | | Half root length formed |
| (8) | | Late root formation |
| (9) | | Full root length (apex open) |
| (10) | | Full root length (apex closed) |
| | 1 | Evidence of a crypt |
| | 2 | Evidence of mineralisation |
| | 3 | All cusps mineralising |
| | 4 | Infundibulum formation |
| | 5 | Crown formation complete |
| | 6 | Early root formation |
| | 7 | Half root length formed |
| | 8 | Late root formation |
| | 9 | Full root length (apex open) |
| | 10 | Full root length (apex closed) |

*Fig. 7. Outline of tooth development scoring system (adapted from Brown & Chapman, 1991a).*

sample from Richmond Park (n=209). The number and location of where the Mesolithic specimens were examined are listed in Fig. 5.

### *The Scheme*

The method used to age both modern and archaeological specimens identifies ten distinct stages of tooth development common to both species. The progressive development of the crown and root of the mandibular premolars and molars can be readily observed from radiographs (Fig. 6).

These stage numbers were used for scoring and are summarized in Fig. 7. The criteria for each stage are described in greater detail by Brown and Chapman (1991a). The ageing resolution of the scheme was found to be insufficient for roe and red deer under 4 and 8 months of age respectively. This became evident after examining the fragmented mandibles of very young deer from various Danish Mesolithic sites. If accurate seasonal assessments were to be made at these sites, then it would be crucial to improve upon this. The minor refinement involves the assigning of scores to the deciduous premolars prior to root completion. It was found that red deer are born with all deciduous premolars at Stage 7 and roe deer at Stage 8. Stage 10 marks the onset of crypt formation of the permanent premolars at Stage 1. Establishing clear criteria results in objective and relatively unambiguous assessments at each stage of development.

For mandibles with complete dentition, these stage numbers are totalled to provide an overall score. If deciduous teeth are present, their scores are added together in exactly the same way and recorded in brackets next to the permanent tooth score, for example 20(27). Incomplete jaws are common archaeologically and the individual premolar or molar scores are of equal significance. Comparisons between the modern known age and archaeological scores provide an accurate indication of kill date. In red deer dental maturity occurs between 40 and 43 months, but ageing resolution decreases after 30 months of age. Loss of resolution in roe deer is minimal as dental maturity is completed in 15 months and ageing by this method remains consistently accurate. A high level of ageing accuracy is still possible

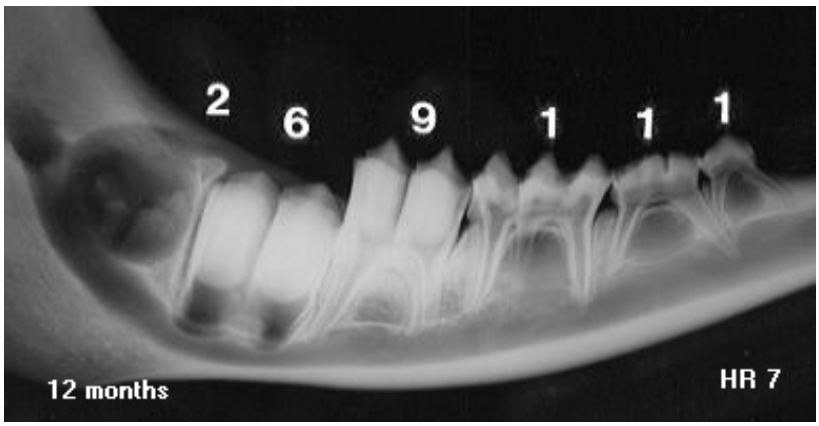


*Fig. 8. Radiograph of a red deer mandible (horizontal ramus) showing molariform dentition at different stages of development.*

from loose teeth, due to the fact that the stage at which a tooth passes through can be very diagnostic of a particular age or range. For example, a single lower third molar of a red deer at Stage 5 (crown formation complete but with no visible root formation) is always between 16 and 18 months of age according to the modern comparative collection. Some examples of these stages of development can be seen in Fig. 8, the tooth development score for this specimen is 20.

All the modern tooth development scores have been broken down into manageable tables (Figs 9–12), each of which will assist in the subsequent interpretation of tooth development scores from archaeological specimens of unknown age.

Developmental stages can be very diagnostic of particular ages or age ranges and often deer of the same age have identical tooth development scores. This can be difficult to represent graphically, but is very important to know. Figs 9 and 11 list the number of red deer which have deciduous premolars, permanent premolars and molars at particular stages of development. Figs 10 and 12 list the same information for roe deer. The ages in months from birth to dental maturity form the '*y*' or vertical axis, and the tooth development scores from (7) to (10) and from 0 to 10, for premolars and molars respectively, form the '*x*' or horizontal axis. The numbers in the tables are in a coded sequence in parentheses for the three deciduous premolars (e.g. (4–1–3)), and in a coded sequence without parentheses for permanent premolars or molars. These represent the number of teeth in the sample that are of a certain age and at a particular stage of development. The age range of any molar or premolar can be read-off for any stage of development. The final age estimation of the specimen is within the age range that is common to all the teeth being examined. Loose developing teeth can also be aged in this way. Seasonal indicators down the right-hand side provide a guide as to when the deer died at any given stage of tooth development.

The development of the three mandibular deciduous and permanent premolars appear to progress at similar rates. This is particularly true of $P_4$ and $P_3$, whereas $P_2$ is sometimes ahead or behind in developmental terms. As a result it is very difficult to assess the age of older, but still dentally immature, red deer based solely on the premolar evidence. From *ca.* 18 months onwards, the age ranges for all three premolars bridge two or more seasons, reducing ageing resolution considerably. For calves in their first year, developmental progression is slightly staggered and ageing using premolars is easier. Nevertheless, confident age determination requires the presence of one or more permanent molars.

In contrast to the premolars, the development of $M_1$, $M_2$ and $M_3$ in red deer advances at very different rates. At *ca.* 16 months the development of $M_2$ 'catches up' with $M_1$ when both are close to maturity (Stage 9). However, it takes another year before $M_3$ also reaches this stage, by which time $M_1$ and $M_2$ are fully formed (Stage 10). A year later, around 38 months of age, $M_3$ also reaches Stage 10 and the permanent molars achieve full dental maturity. Even in these 'older' age stages, prior to dental maturity, a degree of age determination is possible. However, the highest resolution occurs during the first two years of life when marked developmental differences between the three molars are evident. This can be seen in Fig. 11. The combination of molar and premolar scores within this age range provides clear ageing indicators to within one or two months.

Like red deer, the development of both deciduous and permanent premolars in roe deer progress at similar rates but over a much shorter time period. The observations made for red deer also apply to roe deer, but despite uniformity of progression, specific stages are very diagnostic of two to three month age ranges in roe deer. It is not until *ca.* 12 months of age, and close to dental maturity, that ageing resolution decreases. Similar to red deer, it is the second premolar that is occasionally retarded or advanced in relation to the other two premolars. The

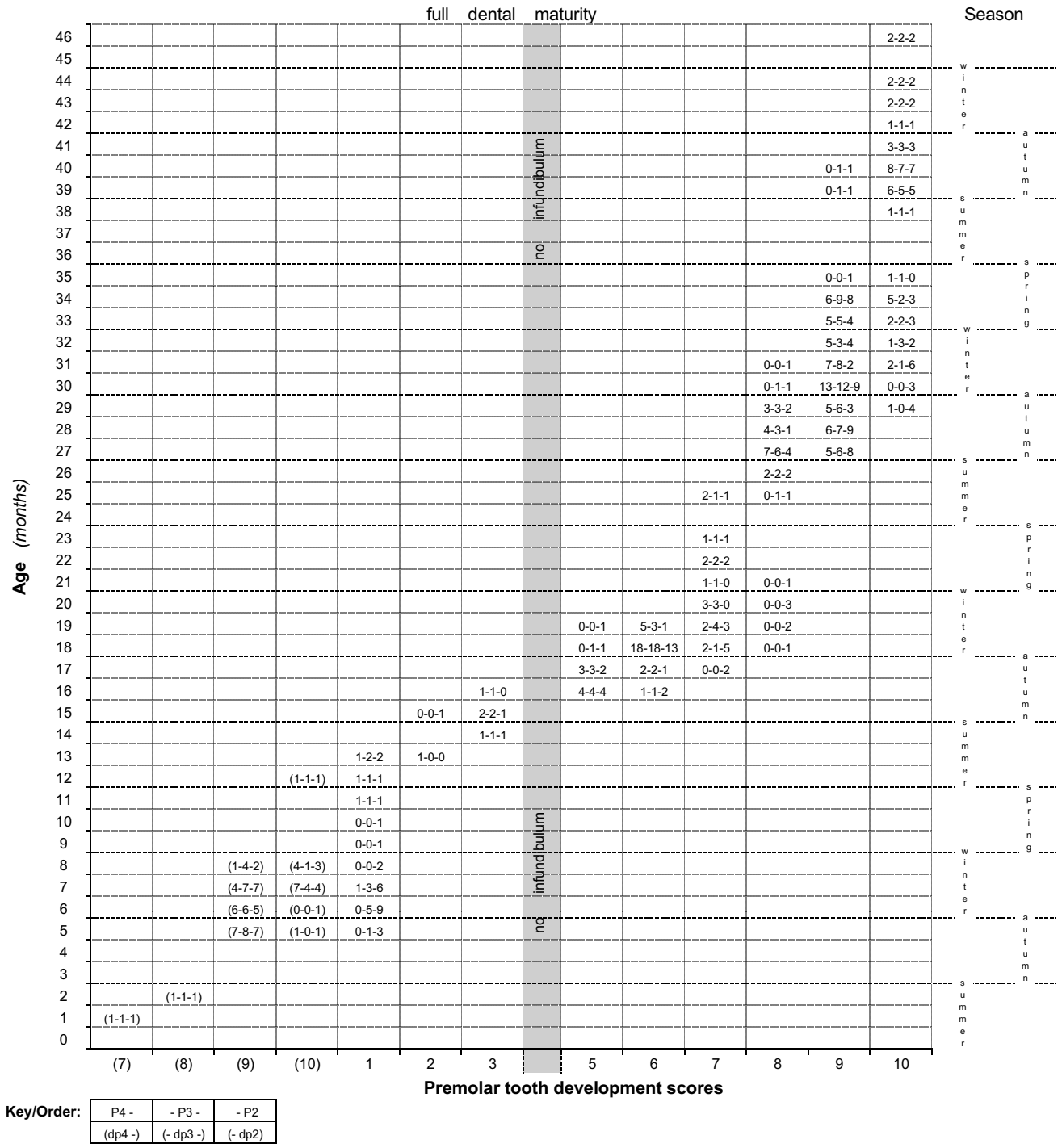


*Fig. 9. The number of deciduous and permanent premolars at different stages of tooth development based on four modern populations of known-age red deer.*

progressive stages of molar development in roe deer are, like red deer, clearly staggered up to Stage 9 thereby facilitating age assessments. Dental development may be complete by six months on $M_1$ and on $M_2$ only three months later. However, $M_3$ remains an excellent indicator of age up to full maturity at *ca.* 16 months. Once again it is the combination of both premolar and molar scores that will provide the best assessments of age.

The reality of the archaeological record is that mandibular dentition is rarely found complete. By breaking down the modern tooth development scores in this way reasonable age assessments of single teeth or

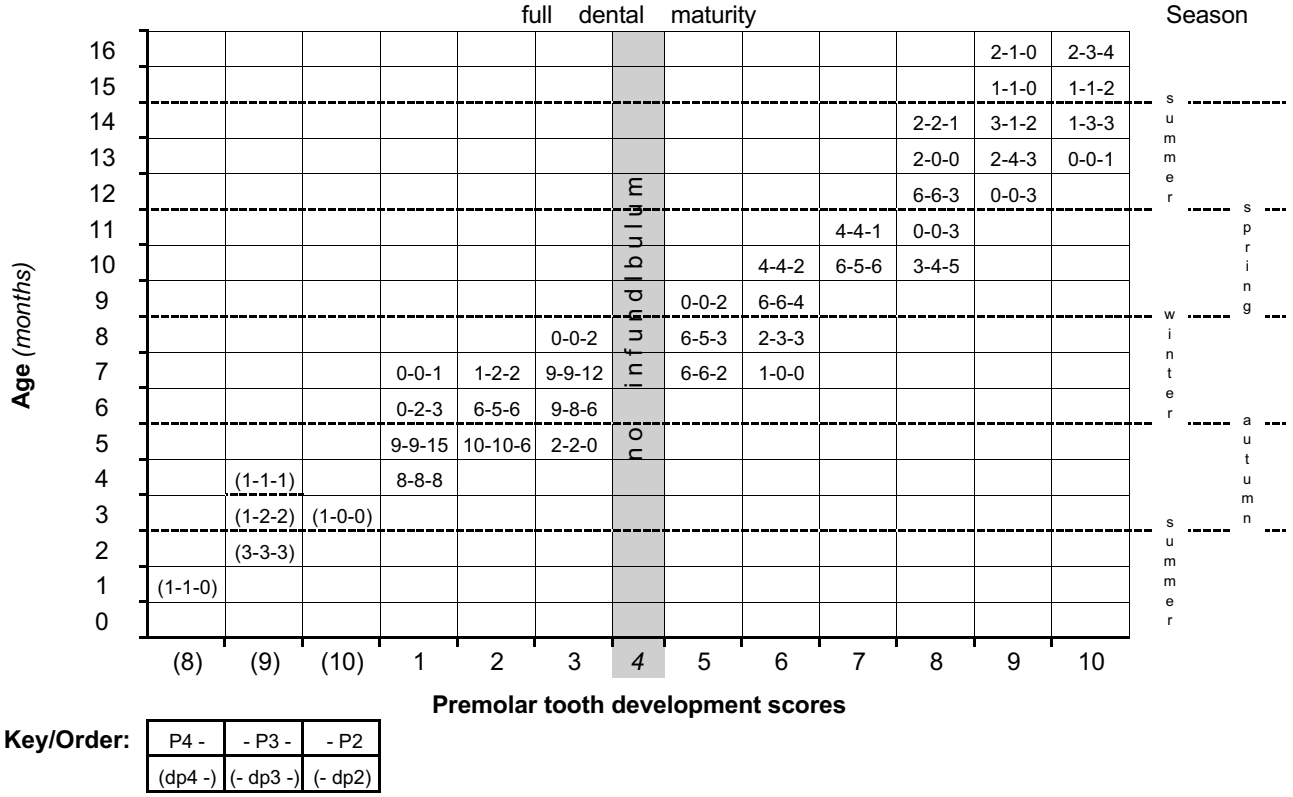


*Fig. 10. The number of deciduous and permanent premolars at different stages of tooth development based on seven modern populations of known-age roe deer.*

fragmented incomplete mandibles are possible. As discussed above, teeth at particular stages of development are very diagnostic of specific ages. If part of an excavation strategy is to establish site seasonality, and if red or roe deer material is present, then the careful recovery of developing molariform dentition should be an important objective.

### *Two examples of estimating the age of mandibles*

The tooth development scores from a red and roe deer will be used to show how the modern dataset and aforementioned figures can provide an estimation of age at death.

Case 1: Fragmented red deer mandible with $M_3$, $M_2$, $P_4$ and $P_2$ present: Stages 6, 8, 6 and 7, respectively.

*Premolars (Fig. 3.9)*

– $P_4$ is represented first in the coded sequence in the table and $P_2$ at the end of the sequence, and it is known that they are at Stages 6 and 7, respectively. The number of specimens at these stages of development can be found above the respective stages numbers along the x-axis. The ages of these specimens are then read off along the y-axis.
– For example, there are 1, 2, 18 and 5 fourth premolars at Stage 6 aged at 16, 17, 18 and 19 months, respectively. For $P_2$ there are 2, 5, 3, 2, 1 and 1 specimens at Stage 7 aged at 17, 18, 19, 22, 23 and 25 months, respectively.
– Because two teeth at different stages of development are being considered, it is necessary to identify where both $P_4$ at Stage 6 and $P_2$ at Stage 7 occur together along the same age row, albeit in different columns.
– This occurs at ages 17, 18 and 19 months. The age at death range for the premolars is therefore 17 to 19 months.

*Molars (Fig. 11)*

– $M_3$ (first in the coded sequence) at Stage 6 occurs between 17 and 20 months whilst $M_2$ (second in coded sequence) at Stage 8 occurs between 16 and 20 months. However, they only appear together between 17 and 20 months of age. This would be the age range if only molars were being assessed.
– But with two age ranges (Premolars: 17–19 months, and Molars: 17–20 months) the only ages at which all the teeth occur together are between **17 and 19 months**.

Case 2: Complete roe deer mandible with $M_3$ at Stage 6, $M_2$ and $M_1$ at Stage 10 and all premolars at Stage 7 (Fig.

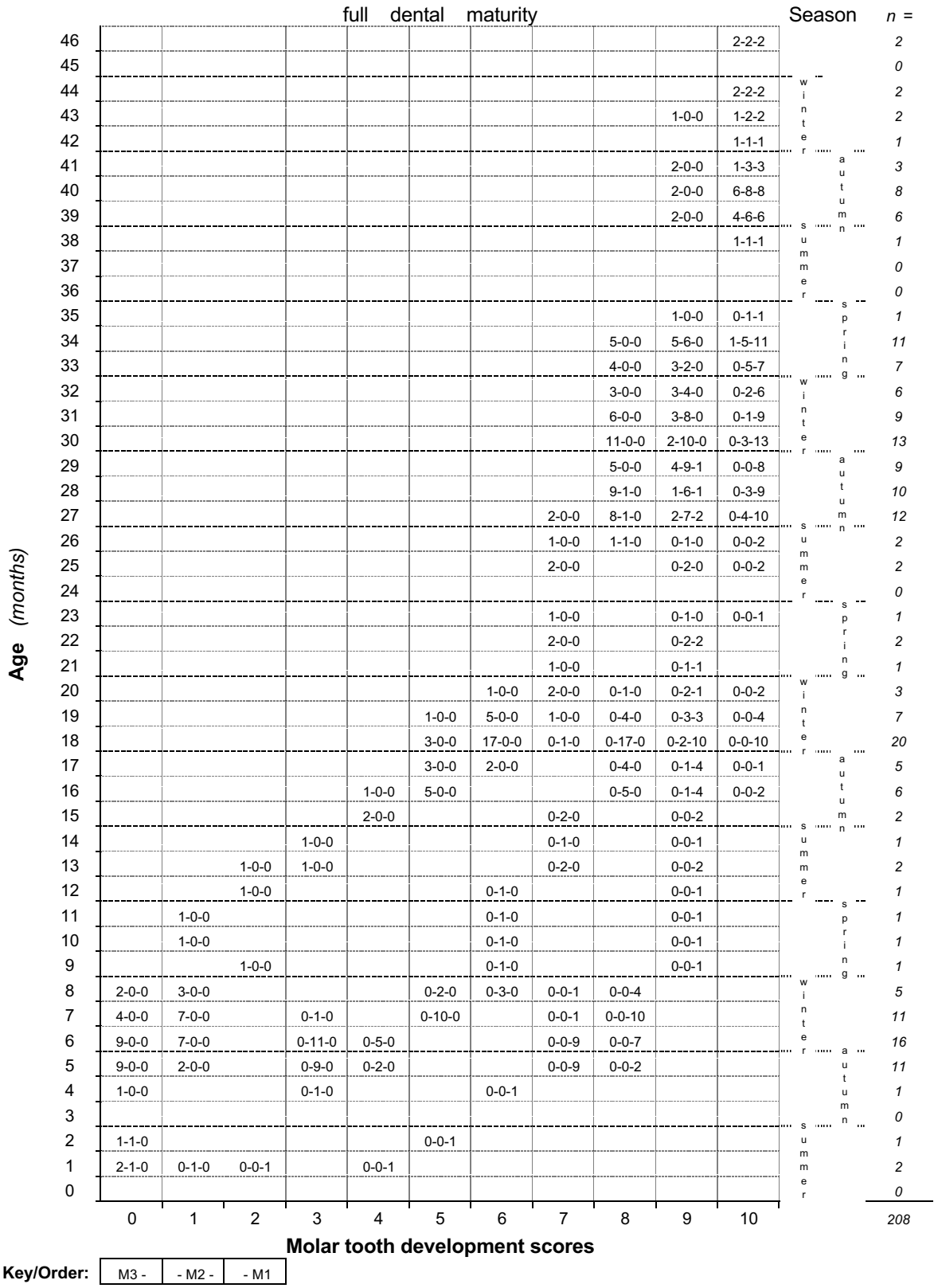


*Fig. 11. The number of permanent molars at different stages of tooth development based on four modern populations of known-age red deer.*

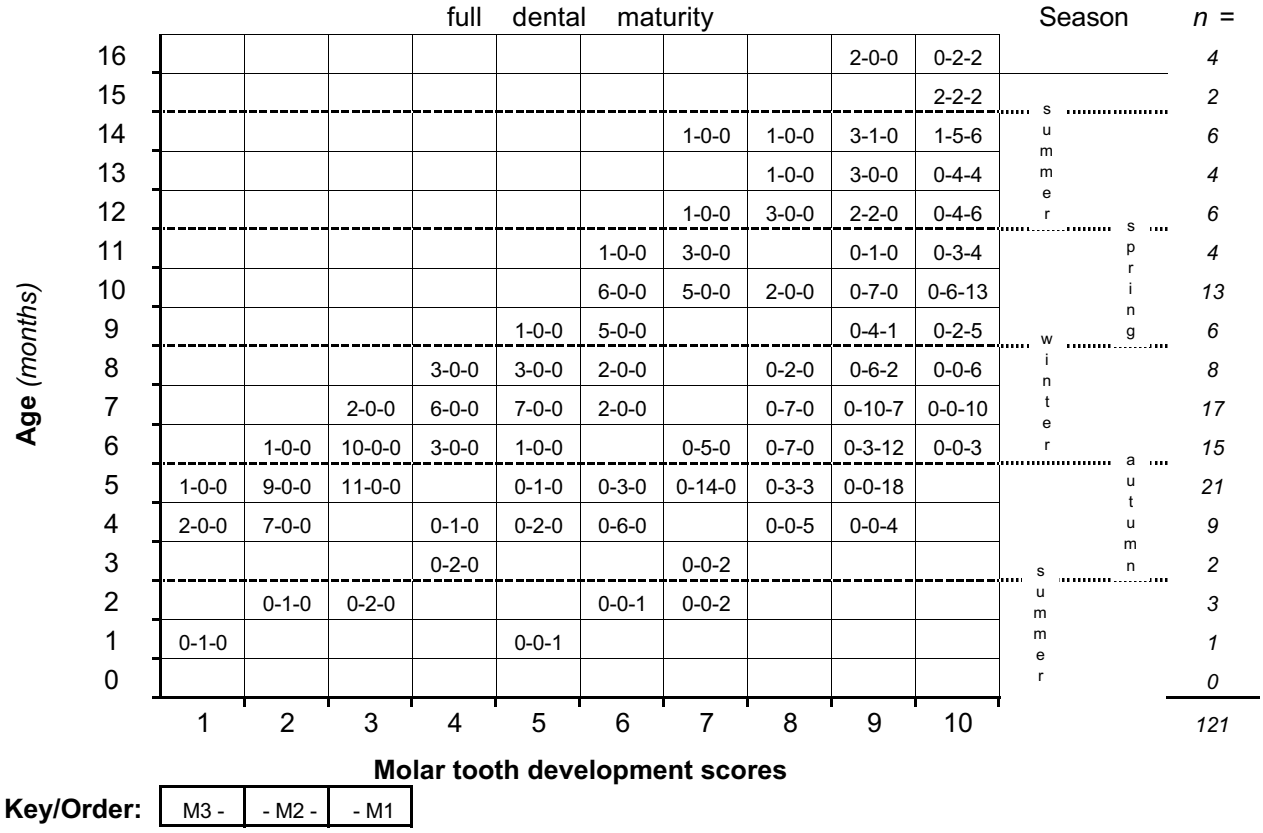


*Fig. 12. The number of permanent molars at different stages of tooth development based on seven modern populations of known-age roe deer.*

13). Same procedure as before, but this time using Figs 10 and 12.

*Premolars (Fig. 10)*

– There are 6 and 4 fourth premolars at Stage 7 aged 10 and 11 months, respectively. For P3 there are 5 and 4 specimens at Stage 7 also aged 10 and 11 months, respectively. Finally for P4 there are six and one specimen aged 10 and 11 months, respectively.
– In this case all three premolars are at Stage 7 between 10 and 11 months of age.

*Molars (Fig. 12)*

– M3, represented first in the coded sequence, at Stage 6 occurs between 7 and 11 months of age. M2 (second in coded sequence) and M1 (third in coded sequence) at Stage 10 occurs between 9 and 16 months and 6 and 16 months, respectively. However, all three only appear together between 9 and 11 months of age. This would be the age range if only the molars were being assessed.
– With two age ranges (Premolars: 10–11 months, and Molars: 9–11 months), the only age at which all the teeth are at these stages together is between **10 and 11 months**.

This method takes into account all the surviving dentition and provides a range of ages that may feasibly contain the combination of tooth development scores. With 208 red deer and 122 roe deer specimens from a diversity of populations in the modern comparative database, it is probable there are sufficient numbers for the assessments to be reasonably valid. The final stage in the analysis is to convert these ages into months of death based on a birth date of June 1.

### *Time of birth*

Important to the ageing of archaeological specimens is the assessment of birth date. The birth timings of modern red and roe deer have been reviewed and discussed in the Star Carr papers and the author's thesis (1997, 1998 and 2001c). It has been assumed that the period from the end of May to mid-June would also be the probable birth dates for the majority of red and roe deer from Mesolithic south Sweden. It is acknowledged that favourable environmental conditions may bring the mean birth date

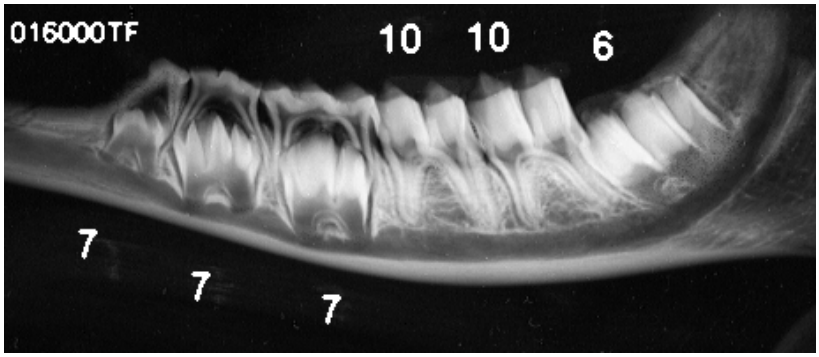


*Fig. 13. Radiograph of roe deer mandible 016000TF, aged approximately 10 months, from the Dourdan Forest, N. France.*

forward by a few weeks but this would have minimal impact on subsequent seasonal assessments.

## Results

Traditional and new seasonality estimates at the 14 sites are compared in Figs 22 and 23. The results will be briefly discussed and an assessment of site function proposed where possible. Radiographs of modern and archaeological specimens have been compared at some of the sites. Examples have been deliberately selected which do not appear in any previous publications. For a more detailed discussion of results and interpretations, the reader is referred to the accompanying references.

*Star Carr*
*(Carter 1997, 1998)*
The proposed spring occupation of the site (Legge and Rowley-Conwy 1988; Mellars and Dark 1998) has been confirmed by these results. However a single roe deer may have been killed as early as February. If so, it supports a more certain winter death of a red deer killed between November and January. The 'spring' and 'winter' deaths of these very young deer provide the best seasonal resolution of all the specimens examined. There are other red deer, whose age at death has been estimated between 27 and 34 months (September to April), which may have been killed in the winter, but may also be autumn or spring deaths.

Using the dataset and method described, the age range for specimen 339L from Star Carr in N. Yorkshire has been estimated between 17 and 19 months (Fig. 14). This has been compared with a modern specimen, G2017F, aged approx. 19 months (Fig. 15). Root development of $M_3$ on 339L may be nearing Stage 7 (half-root length). This makes little difference as from the aforementioned tables the vast majority of known age $M_3$ and $P_4$ have roots at Stage 6 or 7 between 17 and 19 months of age. Death occurred sometime between November and January.

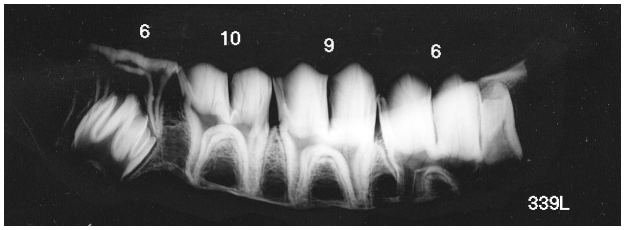


*Fig. 14. Radiograph of red deer mandible 339L from Star Carr, with a proposed age at death of 17–19 months.*

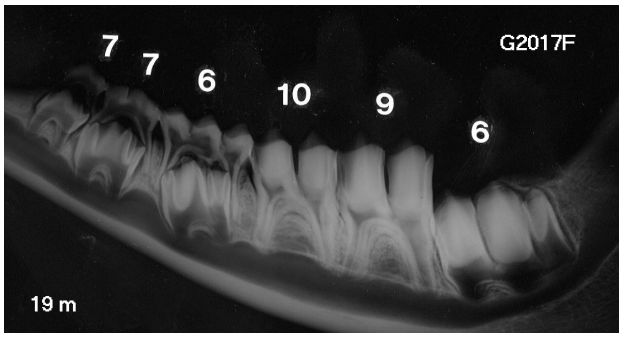


*Fig. 15. Radiograph of red deer mandible G2017F, aged ca. 19 months, from Grizedale, Cumbria, England*

Interpretations of site function range from those supporting a base camp type model to those proposing short intense periods of specialised activity. The new winter evidence now indicates human activity at the site during most of the year. This may be intermittent, brief occupation throughout the year or more permanent presence by some, if not all, of the group. The criterion that sedentary occupation can only be considered at sites where the late winter and spring resource gap has been closed (Jacobi 1987) appears to have been met at Star Carr. This is not to discount evidence of industrial type

activity and interpretations of body part representation (Legge and Rowley-Conwy 1988). But these tasks may have been regularly performed as base camp type activities (Mellars and Dark 1998) in specific activity areas.

*Thatcham*
*(Carter 2001a)*
The results indicate that red deer were killed during the autumn, winter and possibly late summer (Fig. 22). The winter and autumn evidence contradicts the summer-only occupation proposed by Smith (1992). Like Star Carr, this site also appears to have been visited or occupied during the cooler months of the year. The autumn/winter deaths of red deer are not concentrated within one age group but occur in the first, second and possibly third years of life. This may indicate seasonal human presence at the site solely to kill red deer. The new seasonal evidence appears to support the suggestion by Mellars (1976) that river valley sites may have made ideal winter settlements. Neither do the results conflict with the proposal that Thatcham was a short-term home base occupied by semi-sedentary groups (Bradley 1978; Healy *et al.* 1992).

*The Holmegaard complex*
*(Carter 2001b)*
The new results from Holmegaard I, IV and V indicate that red and roe deer were being killed during the warmer months of the year (Carter 2001b). This supports the views of Broholm (1924), Blankholm (1987) and Rowley-Conwy (1993) that these sites were possibly summer hunting camps. A mandible with complete dentition (H-V/CER1) was estimated to be aged 15 or 16 months and killed during the autumn (September or October). The stages of tooth development on this mandible have been compared to a specimen of known-kill date (14.10.97) from Grizedale Forest, Cumbria aged *ca.* 16 months in Figs 16 and 17. It can be clearly seen that the stages of development are virtually identical.

*Mullerup Syd*
*(Carter 2001b)*
Despite the many roe deer bones recovered from the site, only a few specimens could be aged from tooth development. Fortunately, these were from young individuals and were excellently preserved. The results indicate seasonal killing during the spring and summer months. There are many similarities between this site and those at Holmegaard, for example, the faunal composition (Broholm 1924) and ages at which roe deer were killed. (Carter 2001b). Mullerup Syd may also have been a summer hunting camp. But, in contrast to Holmegaard, levels of $\delta^{13}C$ in human bone clearly indicates high intake of marine food (Fischer 1993). It may be significant that Mullerup Syd was only *ca.* 15 km from the sea whereas Holmegaard was *ca.* 55 km away. Unfortunately, the dearth of evidence at Holmegaard and Mullerup frustrates attempts to make sense of these differences and similarities.

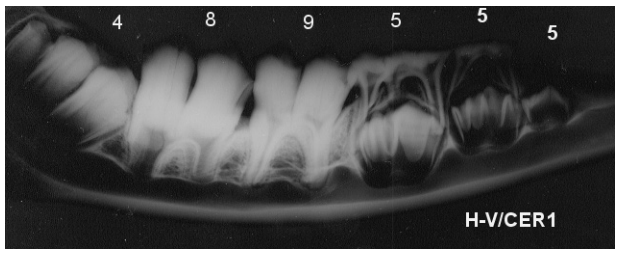


*Fig. 16. Radiograph of red deer mandible H-V/CER1 from Holmegaard V, with a proposed age at death of 15–16 months.*

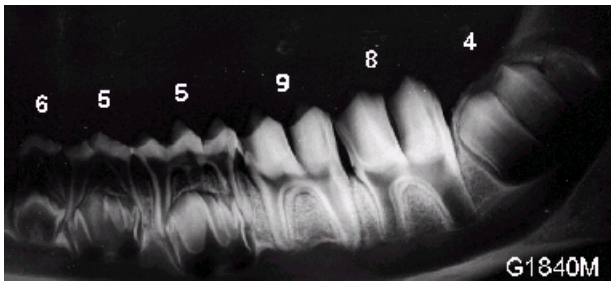


*Fig. 17. Radiograph of red deer mandible G1840M, aged ca. 16 months, from Grizedale, Cumbria, England.*

*Tågerup*
*(Carter in press)*
There is evidence during the early Kongemose (phase I, see Fig. 1) that roe deer were killed throughout the year, apart from possibly early spring. The limited red deer evidence is more ambiguous with a three-year-old killed sometime between August and April. Tågerup may have been occupied year round during the Kongemose culture period.

*Segebro*
*(Carter in press)*
New seasonal evidence comes from the age estimations of red deer based on three loose teeth and a complete mandible. The single teeth are in the early stages of development and indicate death of two calves and a yearling sometime between September and December. The mandible is from a two-year-old, which may also have been killed during this period. It is possible the site was a seasonal hunting camp, but finds of highly decorated flint, bone and antler indicate activities often associated with a base camp. The seasonal evidence may indicate abandonment of the site and a residential move elsewhere during the summer months.

*Ageröd V*
*(Carter in press)*
Despite the poor number of roe deer reported by Lepiksaar (1983) there are some mandibles from Ageröd V that have provided seasonal indications. The estimated ages of three dentally immature specimens indicate summer deaths, similar to Holmegaard and Mullerup Syd. Like Holmegaard, water levels during the winter may have restricted occupation to the drier and warmer months of the year and the site may also have been a seasonal hunting camp.

*Skateholm I*
*(Carter in press)*
The only new seasonal evidence comes from the spring death of a roe deer kid. It is very friable and was difficult to x-ray. Despite fragmentation, it is thought that two of the teeth are at stages of development diagnostic of the age range 10–11 months. This specimen has been compared with a modern mandible in Figs 18 and 19. The new evidence does not necessarily contradict other winter indicators found at the site and supports the autumn to spring bird and fish evidence (Rowley-Conwy 1998). There appears to be no summer indicators at the site and autumn to spring may have been the period of occupation.

*Bökeberg III*
*(Carter in press)*
In this study, the age at death of three red deer calves have provided the best seasonal information spanning the winter period November to February. A two-year-old red deer may have been killed anytime between August and April. Age estimations of other red and roe deer indicate a wide range of ages killed but are of insufficient resolution to provide any seasonal information. Evidence that humans were also present during the warmer months may indicate semi- or permanently occupation of the site for most of the year.

*Tybrind Vig*
*(Carter 2001b)*
The best ageing evidence comes from a red deer calf and four yearlings. The results indicate death may have occurred during the summer and autumn months. The site may have been a temporary hunting camp for the seasonal killing of red deer between June and October (Rowley-Conwy 1994–5). It is possible that some of the older red deer were killed during the winter, but the evidence is less sound.

*Ringkloster*
*(Carter 2001b)*
A newborn roe deer may have died in May, but the main evidence indicates killing of red deer sometime during the summer, autumn and possibly winter months. The new summer evidence increases the times during the year when humans were present at the site. This may indicate a base camp type function rather than a winter hunting camp, as traditionally thought.

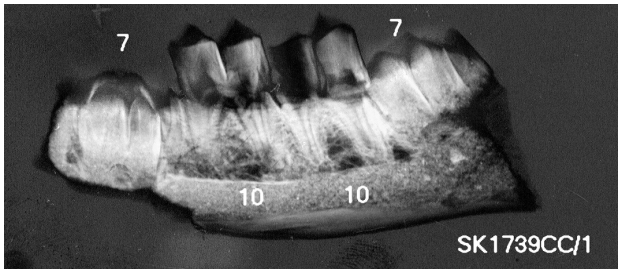


*Fig. 18. Radiograph of roe deer mandible SK1739CC/1L from Skateholm I, with a proposed age at death of 10–11 months.*

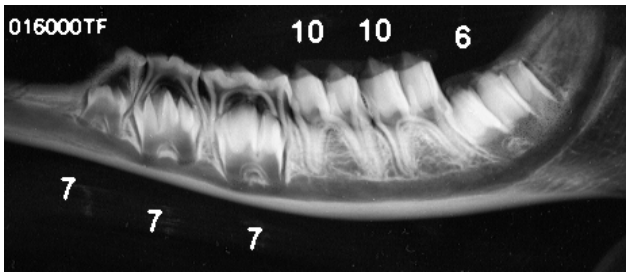


*Fig. 19. Radiograph of roe deer mandible 016000TF, aged approximately ten months, from the Dourdan Forest, N. France.*

*Ertebølle*
*(Carter 2001c)*
Despite the low number of red and roe deer specimens from the 1979–84 excavations examined here, the ageing resolution is high. The age estimations of three mandibles from newly born red deer and the juvenile roe deer evidence indicate that all were killed sometime between February and October. A specimen from one of the newborn red deer (Fig. 20) has been compared with a modern specimen aged one month (Fig. 21). The most concentrated period within which all these deer could have been killed is between April and August. There appears to be a lack of winter evidence at the site, but a stable settlement system over a long period of time has been proposed by the excavators (Andersen and Johansen 1986) and year-round presence is more likely than abandonment during the winter.

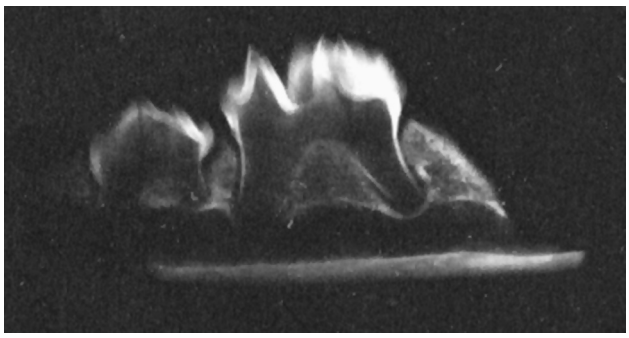

*Fig. 20. Radiograph of $dp_2$ and $dp_3$ from red deer mandible E2168ABVZ/L from Ertebølle, with a proposed age at death of 0–1 month.*

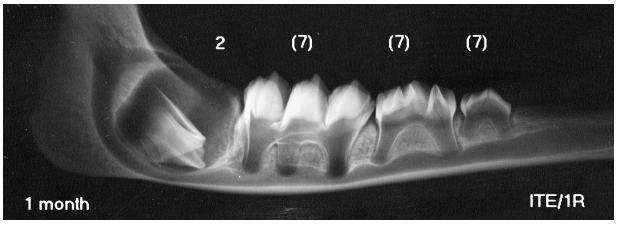


*Fig. 21. Radiograph of red deer mandible ITE/1R, aged ca. one month, from Banchory, Scotland.*

## Settlement patterns revisited

There has been a sufficient amount of new evidence from this research project to re-examine the models of early and late Mesolithic settlement and subsistence reviewed earlier. It is acknowledged that the remodelling process is reliant on evidence derived from sites whose main criterion for selection was the availability of mandibular bone and teeth from two species of deer. Nevertheless, it is felt that the ubiquity of red and roe deer throughout Mesolithic NW Europe and their appearance at most sites provides an indication of their importance to Mesolithic communities. Both species adapted well to the changing early postglacial environment and appear to have been regularly exploited throughout the Mesolithic era. By studying these species of deer it is possible to gain valuable insights into human patterns of settlement and subsistence.

For some deer it has been possible to establish age at death to within a few months and evidence of seasonal human presence at some sites has been obtained. The revised seasonal evidence at each of the sites under consideration has been compared in Figs 22 and 23 to the traditional assessments shown earlier (Figs 3 and 4).

### *Early Mesolithic*

The difficulty of modelling settlement during the early Mesolithic and the reliance on evidence from inland sites has been acknowledged. A variety of models were discussed, most of which involved 'highly seasonal patterns of mobility' thereby avoiding over-exploitation of resources. It will be argued here, based on revised site seasonality (Fig. 22) and function that such high levels of mobility may not have occurred. It is acknowledged that residential movement may have been the preferred option amongst Preboreal and Boreal groups and it will not be assumed that new seasonal evidence must be an indication of increased sedentism (Hitchcock 1982; Binford 1983; Price and Brown 1985).

It was proposed earlier that seasonal mobility may have involved residential movement between short-term inland summer sites and longer-term coastal or river valley base camps. Any winter seasonal evidence would now be submerged at the latter sites. The results from this study indicate human presence at some inland sites during the winter months and revision of this settlement model is necessary. There is no doubt that if close enough, the reliability and productivity of coastal biotopes would have created a 'pull-force' (Simmons 1996). Their economic importance is evidenced by the many Swedish and Norwegian Preboreal and Boreal coastal and island settlements (c.f. Nordqvist 1995; Kindgren 1995). But it is thought that inland sites occupying favourable ecological niches (Lewthwaite and Rowley-Conwy 1980) may have been equally attractive to early Mesolithic groups.

At Star Carr, Thatcham and possibly Holmegaard I, winter evidence may indicate increased sedentism often associated with home base function. Revised seasonality at these sites is now similar to that proposed at Mount Sandel (8440± 65 – 8960±70 BP) close to the River Bann estuary in Ireland, which is thought to have been a base camp (Woodman 1985b). It was suggested that Maglemosians may have spent winters not beside lakes but on the banks of what are now submerged rivers (Rowley-Conwy 1987b). Whatever the case, there appears to be increasing evidence that during the British Preboreal at least these resource-rich lowland locations were actively sought out by Mesolithic groups. The lake or riverside location of these sites possibly ensured availability of sufficient resources for occupation throughout the year. Continuous occupation cannot be proven but there may have been an element of semi-permanency in which the sites were always maintained but the number of occupants varied seasonally.

Comparisons with the British Preboreal sites are hindered by a virtual absence of contemporary south Scandinavian sites. The new seasonal evidence from the Danish Boreal sites confirm their 'summer only' status (with the possible exception of Holmegaard I) and may indicate different function to the British Preboreal sites. Local conditions may have restricted occupation to the

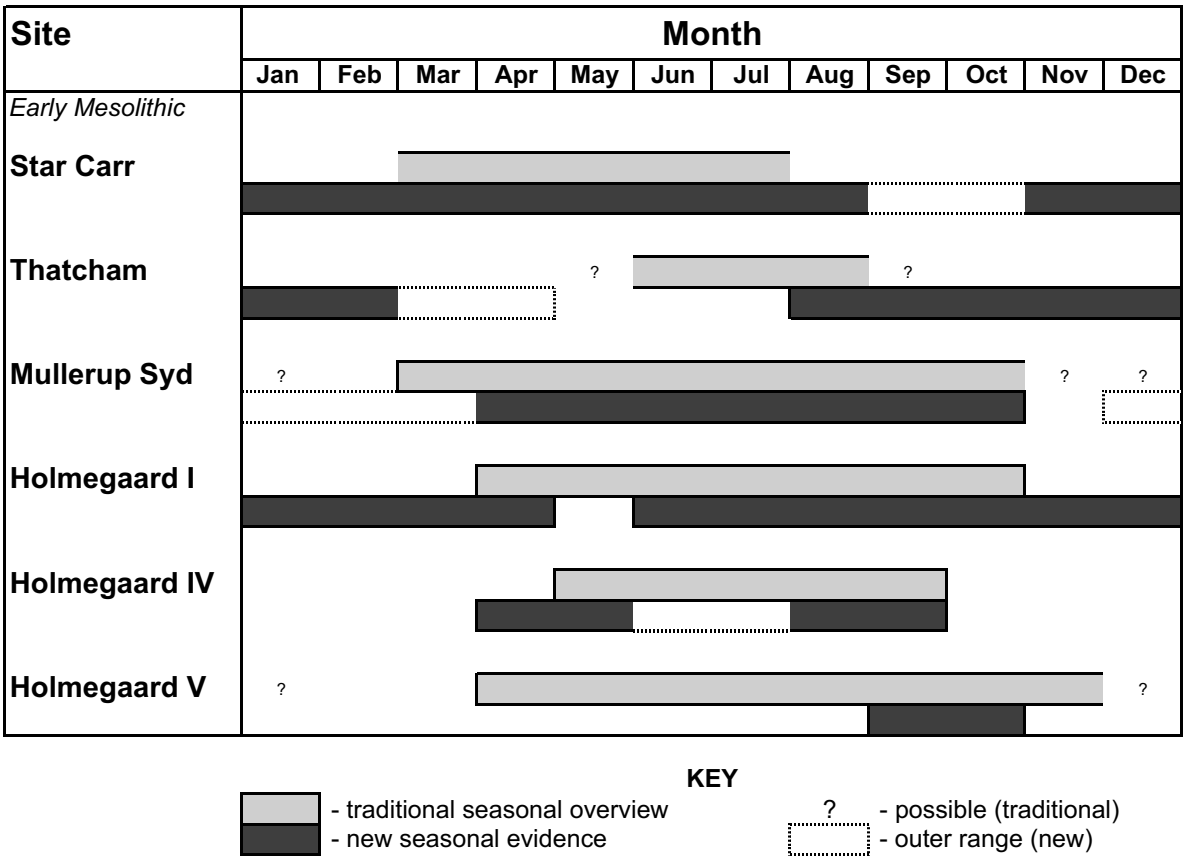


*Fig. 22. Traditional and new seasonal assessments for early Mesolithic site.*

drier summer months, but it may be that sites within the Holmegaard complex may have been occupied at different times, dependant on water levels. Similar seasonal movement may have occurred at the Ulkestrup complex of sites in Denmark (8030±140 – 8370±130 BP) (Richter 1982). A study of prevailing summer and winter wind directions by Grøn (1995) at this complex showed that sites were orientated so as to be protected from seasonal winds. Protection from winter winds is evident at Star Carr (Cloutman and Smith 1988) and examination of the Holmegaard complex may reveal similar site orientations.

The temptation to associate increased seasonal mobility with the earliest phases of the Mesolithic should be resisted. Contact with the coast was likely, despite reservations (Day 1996), but it is possible that Preboreal population size did not warrant exploitation of coastal resources to the extent required later by larger Boreal populations. This may explain the different seasonality at the British Preboreal and Danish Boreal sites. Seasonal evidence at the two Danish Preboreal sites of Favrbo and Skottemarke (*ca.* 8650 – 9150 BP) indicate winter killing of elk (Møhl 1980) and seasonality similar to the two British sites. The abundance of terrestrial and freshwater fauna combined with predictable behaviour and a rich source of plant food may have more than satisfied the needs of Preboreal hunters. Coastal Swedish and Norwegian Preboreal sites, revealed by isostatic land rise, provide evidence of marine exploitation, but they are very small in size. Similarly located sites will no doubt be discovered submerged further south in Denmark and south Scania in due course. But these may also be small and reveal highly seasonal and specialised food procurement activities rather than large base camps that were part of a coastal adapted economy.

The proposal for increased sedentism during the early Mesolithic has been based mainly on evidence of winter human presence at the sites. If human groups are to survive severe periods of shortage in temperate or colder climates and avoid residential movement, then it is crucial that the late winter and spring resource gap is closed (Jacobi 1987). A variety of strategies may be adopted including hunting the over-wintering animals, planned 'seasonal storage' during times of relative abundance (Testart 1982; Spikins 1999), trading with more affluent groups or by the exploitation of lower quality foods (resource generalisation) (Lieberman 1993). A shorter growing season promotes increased storage, reduced residential mobility, greater exploitation of locally orientated resources and logistically organised food procurement. There does appear to be evidence indicating

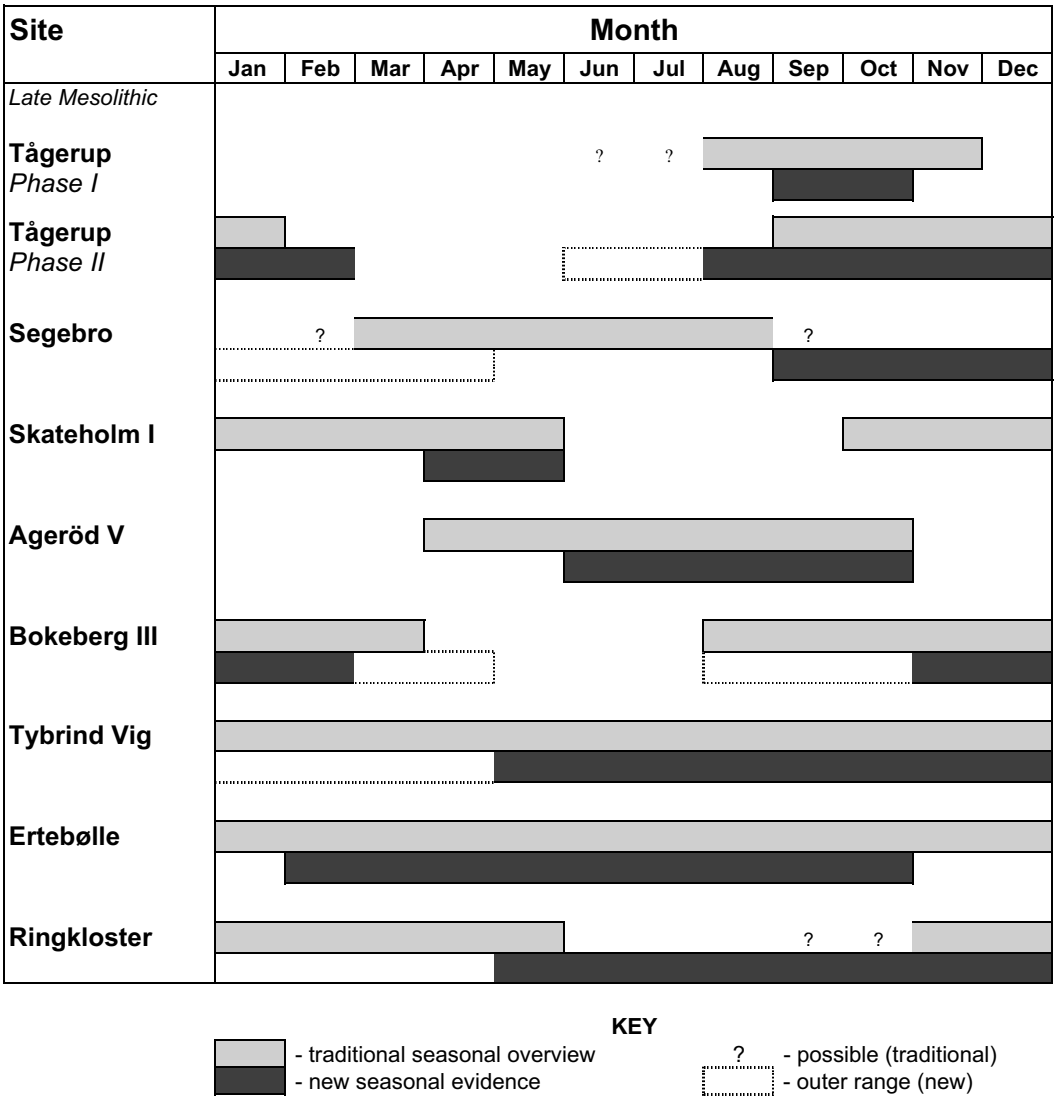


*Fig. 23. Traditional and new seasonal assessments for late Mesolithic site.*

the killing of 'over-wintering' animals at some early Mesolithic sites. It is thought that there would have been a sufficient abundance of red and roe deer in the immediate vicinity of all the sites to allow human occupation during this critical time of the year. At the same time it is acknowledged that seasonal movement cannot be precluded just because an abundant resource base allows increased sedentism (Higgs and Vita-Finzi 1972).

It would appear that early Mesolithic groups were capable of efficiently exploiting the inherent natural abundance of the environment (Lewthwaite and Rowley-Conwy 1980) to such an extent that sedentism became a viable option. Being able to 'collapse residence patterns' (Jacobi 1987) into one location rather than spreading them throughout the landscape demonstrates a strategy of settlement and subsistence which went beyond a mere passive response to seasonal changes (Woodman 1985a).

### *Late Mesolithic*

Two general patterns of settlement and subsistence emerged from the discussion earlier. A significant factor distinguishing the two settlement patterns is the permanent occupation of inland sites. Seasonality at both inland and coastal sites will be examined to test the validity of these models. The sample sizes at most of the late Mesolithic sites are small, but it has been possible to revise seasonality at some sites (Fig. 23). There is now seasonal evidence from Tågerup that coastal sites may have been permanently occupied during the Kongemose. At the nearby and contemporary site of Segebro, new evidence indicates human presence during the winter months and, if combined with traditional seasonal assessments, may also have been occupied year-round. These sites and the later sites of Tybrind Vig and Ertebølle lend support to the idea of increased sedentism at late

Mesolithic coastal sites. Reinforcing proposals that large coastal sites were permanently occupied satisfies a criterion common to both models, but it is seasonality of the three inland sites that may help to clarify any underlying pattern of settlement.

It is acknowledged that in both models logistic mobility was probably involved in extracting resources which were unavailable at or near the parent settlement. There may have been radial movement out from the inland or coastal base camps by task groups to temporary camps at different times of the year. Alternatively, groups from the coastal sites may have adopted linear movement up and down the coast operating within a narrow coastal band (see Simmons 1996; Nordqvist 1995). If any of the three inland sites examined in this study were special purpose camps then it would difficult to determine, based on seasonal evidence, which settlement system they were a part of. But, if seasonal evidence indicates possible year-round occupation, and if the sites are reasonably well inland, there may be justification in proposing that these sites were part of an inland based settlement system.

It is thought that Ageröd V may have been seasonally visited during the summer or autumn and that the nearby contemporary site of Bökeberg III was occupied year-round. Ageröd V is well inland with evidence of coastal links but outside the distance criterion set by Larsson (1980). It is possible that both these sites were part of the same integrated inland settlement system. Evidence at the nearby and contemporary site of Hög in south Scania may support this predominantly terrestrial-based settlement pattern. This site is thought to be comparable with Ageröd V (Iregren and Lepiksaar 1993) and, based on lithic evidence, may have been a short-term hunting camp. There is evidence for the exploitation of terrestrial game and freshwater fish, but an avoidance of the coastal zone, despite being only a few kilometres inland. In contrast, at the inland type site of Kongemosen where there are winter and summer indicators (Fischer 1993), the $\delta^{13}C$ evidence indicates regular exploitation of marine resources (Clutton-Brock and Noe-Nygaard 1990). It would appear that Ageröd V was a special purpose camp, but whether it was part of an inland or coastal-based settlement system is uncertain.

Seasonal evidence at the later Danish site of Ringkloster indicates occupation during the summer, autumn and possibly winter months. Site size and the presence of pottery may indicate a base camp function. Seasonality has been revised at Ringkloster and Bökeberg III and permanent occupation there is possible, but evidence of coastal links and proximity to the coast must also be considered. Both sites were within a day's walk of the coast, but, as has been noted at some early Mesolithic sites and at Hög, this does not mean that marine resources were always exploited. Differential exploitation of coastal and inland resources may have occurred, but with task groups radiating out from an inland base camp to smaller fishing locations dotted along the coast.

It is thought that Ringkloster, like Star Carr in the early Mesolithic, was not a seasonal hunting camp but instead a permanently occupied base camp. Andersen (1994–5) described Ringkloster as an 'inland central site' surrounded by smaller sites. This and other large inland base camps may have operated a radial and logistic settlement pattern whereby smaller inland and coastal sites supported the 'parent' settlement by accessing key resources at different times of the year. The large coastal sites may also have been occupied year-round but operated a linear and logistic pattern of mobility up and down a narrow coastal zone (Simmons 1996). Sites only a few kilometres inland may have been part of this coastal-based settlement system.

The argument that residential movement may have been unnecessary from inland base camps located in 'favourable ecological niches' has been proposed for the early Mesolithic. This may also be the case later in the Mesolithic when terrestrial and aquatic resources would have been just as abundant. Clearly resource availability fluctuated seasonally and seasonal storage is likely to have been important. But, in so far as red and roe deer are concerned, hunter's knowledge of behaviour patterns and the local environment can ensure predictable returns at all times of the year (Carter 2001c). Population pressures may have led to the division of territories, e.g. coastal and inland, resulting in permanent occupation of some inland sites (Larsson 1980). Alternatively, these sites were a continuation of a settlement pattern established much earlier in the Mesolithic.

## Conclusion

Based on knowledge of likely birth dates, it has been shown that tooth development provides a good indication of age in juvenile red and roe deer. The ages at which these dentally immature deer were killed have been used to assess when the Mesolithic sites were occupied. Identifying at what time of the year humans were present at these sites has assisted in clarifying early and late Mesolithic settlement and subsistence patterns. Whilst confirming many existing seasonal indicators, the results also indicate increased sedentism during this important phase of prehistory.

*Acknowledgements*

I would like to thank the following people for granting permission and assistance in examining the material. Richard Sabin, Curator Mammal Group, Dept. of Zoology, Natural History Museum, London, Dr Kim Aaris-Sørensen and Knud Rosenlund from the Zoological Museum, Univ. of Copenhagen, Dr Søren H. Andersen of the Marinarkaeologiske Forskningscenter, Roskilde and staff of the Conservation Dept, Univ. of Arhüs, Moesgård. From Sweden, Lars Larsson and Ylva Olsson of the University of Lund, Per Karsten of the

Riksantikvarieämbetet, Lund and Ingmar Billberg of Malmö Museum. I am indebted to Ola Magnell, Peter Heath and in particular Professor Ken Thomas of the Institute of Archaeology, University College London for their advice and encouragement. The visits to Denmark and Sweden were made possible by awards from the Central Research Fund of the Univ. of London. A research grant from the Institute of Archaeology, UCL provided funds for examining the British specimens. I am grateful to the Institute for Aegean Prehistory for a travel grant which supported accommodation expenses at the ICAZ 2002 conference.

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*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 62–67*

# 4. The Table Test: a Simple Technique for Sexing Canid Humeri

*Deborah Ruscillo*

*The Table Test was developed by the author in 1999 for sexing archaeological canid remains. A complete adult humerus of a fox or dog is placed on a level surface and, based on the morphology of the deltoid tuberosity, will fall over or remain steady on its anteroventral side. T-test and contingency table results reveal that this method can identify male dogs 85% of the time, and male fox 76% of the time based on a test sample of 128 canids. Although the method is of limited utility, the technique does offer some information about canid remains previously unavailable. This chapter will show results of the study as well as the practical application of this method that can easily be used in the field.*

## Introduction

Determining the sex of domestic dog and other canid remains from archaeological sites is problematic. Canids, such as the dingo, jackal, dhole and wolf can be compared osteometrically to determine sex by a comparison of body size between males and females (Higham *et al.* 1980). Osteometrics, however, are not as applicable to domestic dog remains for determining sex because mixed breeding and human selection, particularly in the past 3000–4000 years (Clutton-Brock 1995), have created vast size differences within the species. It is, therefore, necessary to rely on the examination of sexually dimorphic traits of the canid skeleton to reveal clues about the sex of the animal. The most reliable bone element from which to determine the sex of canid and other carnivore remains is the *baculum*, or penis bone. However, the *baculum* may not be present or preserved with all male canid remains and one cannot assume that the sex of the individual is female simply because the *baculum* is missing.

Existing morphological studies are few and concentrate on the cranium and mandible, for example The and Trouth's (1976) study of sexual dimorphism in the basioccipital portion of the dog cranium, Lorber *et al.*'s (1979) study of the canine teeth of small dogs, and more recently, Kieser and Groenveld's (1992) comparison of the mandibulodental complex of canids. These methods can be complicated and require a significant amount of conjecture when examining the anatomical features pointed out in these studies. Furthermore, these studies can be useful only if the cranium and/or mandible of the canid is available and intact.

This paper presents a simple technique for sexing canid humeri that may be useful to the zooarchaeologist and archaeologist when examining archaeological remains of canids. This technique will be especially useful when examining domestic dog remains rather than feral canids, because the examination of domestic animal bones can shed light on human selection patterns. Dog burials are often encountered in archaeological sites, even dog cemeteries (see Brothwell *et al.* 1979; Day 1984; Stager 1991; Wapnish and Hesse 1993; Hamilakis 1996). Particularly with social and cultural features like these, a method for determining the sex of the carefully buried individuals might provide some clues about the animals and their relationship with the occupants of a site. In general, the examination of sex selection patterns of working dogs and companions is relevant when in-

vestigating the history of the human/dog relationship in any context.

### The Collection

Red fox (*Vulpes vulpes*) and domestic dog (*Canis familiaris*) skeletons of known sex were studied from modern osteological collections in Canada (Royal Ontario Museum, and the University of Toronto), and the United Kingdom (Ancient Monuments Lab of English Heritage, the British Museum of Natural History, Southampton University, Bradford University, York University, Sheffield University, the Creswell Crags Visitor Center, Glasgow University, and Edinburgh University). Accordingly, it was important to establish a study collection of domestic dogs that would account for size, age and morphological variation to determine the utility of the method for various breeds, especially in archaeological contexts where breed is usually unknown. The total number of specimens examined for this study was 128: 72 foxes (37 males and 35 females), and 56 dogs (32 males and 24 females). Of the 56 specimens of domestic dogs, 34 breeds were examined representing all size ranges and skeletal morphologies. All specimens were over one year of age, some domestic dogs were as old as 15 years. Six wolves were also examined for this study but this sample size was too small to produce viable conclusions.

### Technique

This technique can be applied to either the right or left humerus of a canid, provided that it is complete, mature, and without pathology. The humerus is held from the proximal end and placed on its anteroventral plane on a level surface. The humerus will either fall on its medial side (Figure 1A), or stay on its anteroventral side (Figure 1B). The result of laying the humerus down in this manner, resting or falling over, is all the information that is required for estimating the sex of the individual. If the humerus falls over onto its medial side, it is likely a male individual. This, however, does not necessarily mean that if the humerus rests on its anteroventral surface, it is likely a female. When the table test was performed on both the right and left humerus of each of the 128 specimens, 62% of male fox humeri and 28% male dog humeri rested on their anteroventral side. In other words, if the humerus rests, it could be either male or female and the test remains inconclusive, particularly for fox specimens. However, 78% of the fox humeri that fell over were male (Figure 2), and 85% were males in the case of domestic dogs (Figure 3). In general, the method works better for dogs, particularly because almost 70% of the humeri that rested were female. The test therefore can also suggest female dog

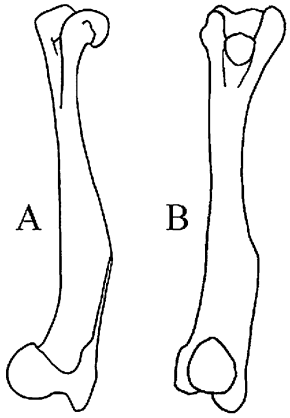


*Fig.1. Canid humeri showing (A) lateral perspective, and (B) posterodorsal perspective.*

identifications, albeit with less confidence than that of male identifications.

The results of the Table Test have been summarized in the contingency tables below for fox and dog separately. Figure 4 shows the results of the fox table test for the left humerus (the right humerus reflected identical results). The test reveals that 78% of the humeri that fall over are male and only 22% are female. The humeri that rest on their anteroventral plane do not show a significant separation between the sexes, though females tend to rest more frequently than males. **The humerus falling over is the important event to measure in these tests to suggest a male over a female identification of a humerus.** Calculations reveal that if a humerus from a red fox falls over during the table test, the bone is 78% likely to be a male individual, or in terms of odds, about 3.2: 1 odds in favour of a male identification. Chi-square ($\chi^2$) calculations reveal a chi-square value of **6.69**. Even with Yates' correction to account for possible error, the value of **5.35** still remains above the critical $\chi^2$ value. The critical value from a chi-square distribution table for one degree of freedom and a probability level of 0.05 is **3.84**, therefore the results show a fairly significant relationship between the sex of the humerus and the phenomenon of falling over. We, therefore, can reject the null hypothesis that there is no relationship between the two variables.

For the domestic dog (Figure 5), the results are more significant. Of the 27 individuals that fell over on the table, 85% were male and only 15% were female. Again, female humeri tend to rest on their anteroventral plane (69% of the resting humeri), but at a more significant ratio (2.5:1). Again, different breeds were used for this experiment to account for the different physiological differences of the humeri in correlation with the variety of shapes and sizes exhibited by the vast array of breed types. Despite the greater variation in size and skeletal

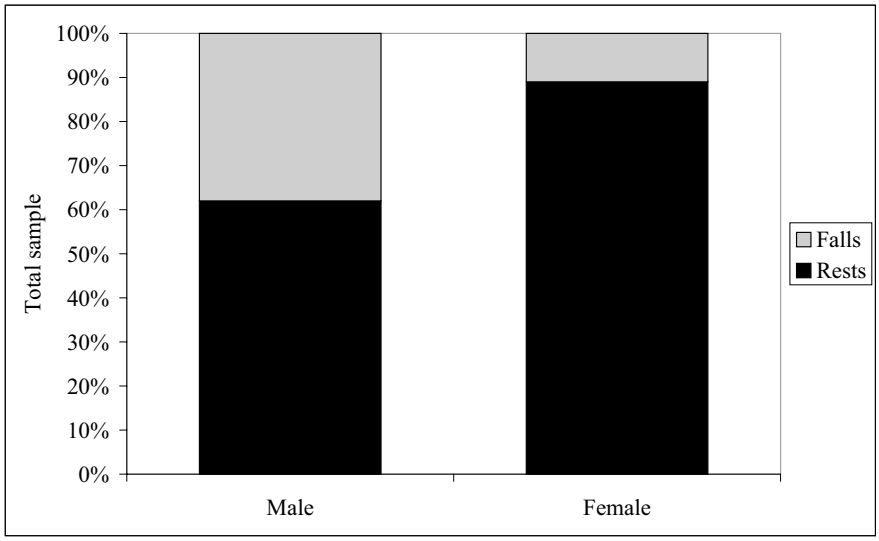


*Fig. 2. Fox table test results.*

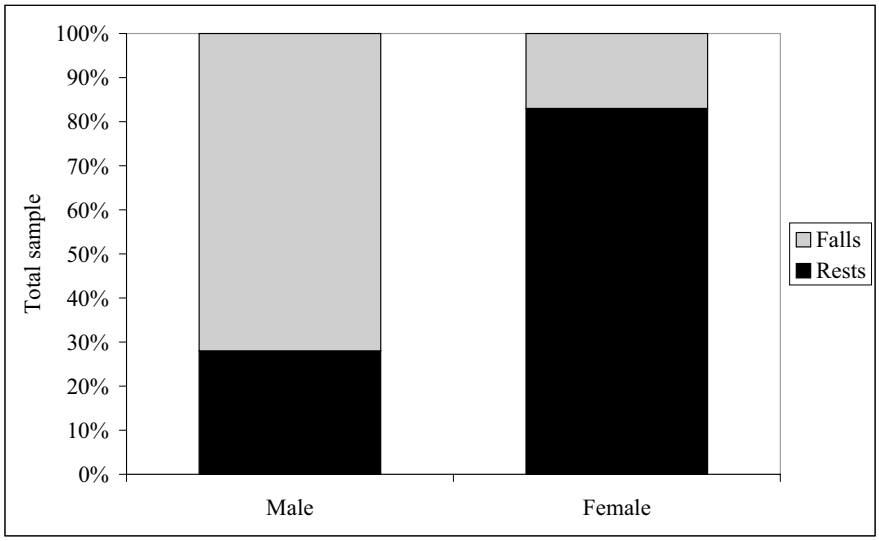


*Fig. 3. Dog table test results.*

morphology of the dogs in comparison with the foxes used in this study, the *Canis* results are more significant. The chi-square value for this set of data for the dogs is **16.73**, or **14.61** after Yates' correction. Again, the critical value for one degree of freedom and a probability level of 0.05 is **3.84** showing a high relation between the sex of the humerus and the event of falling over, with a chi-square value of 16.73. Therefore, if one finds a dog humerus during archaeological excavation, the table test can be applied to suggest the sex of the individual. If the complete adult humerus falls over, there is an 85% chance, or 5.7:1 odds in favour of the humerus being from a male individual. If the humerus rests, there is an almost 70% chance of the humerus being from a female dog.

In summary, the Table Test can suggest a male classification of a humerus that falls over with 78% confidence for red fox, and 85% for domestic dog. If a red fox humerus rests on its anteroventral side, classification cannot be confidently made, however, if a domestic dog humerus rests, there is a 69% chance that the humerus is that of a female individual.

## Discussion

Along the anteroventral plane of the humerus towards

| | MALE | FEMALE | TOTALS |
|---|---|---|---|
| **FALLS** | O = 14.00<br>E = 9.25<br>Row % = 0.78<br>Column % = 0.38 | O = 4.00<br>E = 8.75<br>Row % = 0.22<br>Column % = 0.11 | O = 18 |
| **RESTS** | O = 23.00<br>E = 27.75<br>Row % = 0.43<br>Column % = 0.62 | O = 31.00<br>E = 26.25<br>Row % = 0.57<br>Column % = 0.89 | O = 54 |
| **TOTALS** | O = 37 | O = 35 | N = 72 |

*Fig. 4. Contingency table for fox humeri table test results, where O = observed frequency, E = expected frequency, and N = total number of individuals.*

| | MALE | FEMALE | TOTALS |
|---|---|---|---|
| **FALLS** | O = 23.00<br>E = 15.43<br>Row % = 0.85<br>Column % = 0.72 | O = 4.00<br>E = 11.57<br>Row % = 0.15<br>Column % = 0.17 | O = 27 |
| **RESTS** | O = 9.00<br>E = 16.57<br>Row % = 0.31<br>Column % = 0.28 | O = 20.00<br>E = 12.43<br>Row % = 0.69<br>Column % = 0.83 | O = 29 |
| **TOTALS** | O = 32 | O = 24 | N = 56 |

*Fig. 5. Contingency table for dog humeri table test results, where O = observed frequency, E = expected frequency, and N = total number of individuals.*

the proximal end lies the deltoid tuberosity on which the deltoid muscle attaches. It is the extent to which this tuberosity is developed that determines the stability of the humerus on a level surface. The humerus falls over more commonly for males because of the greater development of their deltoid muscle resulting in a larger, more defined tuberosity on which the muscle attaches. The reason that the deltoid muscle is better developed in males can be explained by examining the behaviour and physiology of male versus female canids. In contrast to cervids and bovids, canids do not have headgear to account for significant weight differences of the cranium to explain the dimorphic differences of the deltoid tuberosity due to loading. Male fox do display, however, greater use of their canine teeth in conjunction with combative behaviour, especially during the mating season (MacDonald 1995). The same is true for all canids. Moreover, in a study of differences of behaviour between the sexes, Hart (1995) showed through statistical analyses, that male dogs of any breed exhibited *ca.* 65% greater aggression towards other dogs than females. Males also showed significantly greater physical activity in general over females, including dominance over owner, territorial defense, destructiveness, playfulness etc. (Hart 1995, 72–73). This exposure to greater stress on the neck and anterior limbs from aggression and play would develop more extensive musculature as well as more robust muscle attachments on bones of the anterior limbs. Males of most canid species and breeds are also slightly larger than the female, in general. The larger body size and weight would develop proportionately larger muscles and corresponding bony attachments.

Direct connections with neck muscles to the humerus are minimal. The exception would be the brachiocephalicus muscle which begins on the transverse processes of atlas and second, third and fourth cervical vertebrae (and on the mastoid process of the temporal bone and the nuchal crest), and extends to deltoid tuberosity and fascia of the shoulder and arm (Sisson and Grossman 1953). This direct link from the neck vertebrae to the humerus would affect the morphology of the deltoid tuberosity in association with the greater brachiocephalicus muscle, but not necessarily the bone ends. The deltoid tuberosity in the fox, for example, has shown significant sexual dimorphism causing the tumbling effect of the male humerus on a level surface as illustrated by the Table Test. The proximal and distal humerus of the fox, meanwhile, do not reveal significant shape differences as revealed during the course of this study.

Figure 6 shows the position of the humerus in the mammalian skeleton. With greater loading or stress on the anterior limbs, the humerus acts as shock absorption with a spring-like effect (Discovery 1999). The position of the humerus, unlike the other anterior long bones, is diagonal in orientation and therefore does not bear weight directly on its ends or shaft. When exposed to loading or stress, the proximal end pivots in the glenoid cavity, while the distal end bends on its condyles to absorb shock. In this manner, weight is not directed to either end of the humerus. Instead, the humerus adjusts itself to absorb strain.

This is perhaps affected by the sexual behaviour of the males, particularly during mating, which could affect the musculature of the humerus, and hence, the size of the muscle attachment. It has been noted, however, that females can occasionally have a larger than common tuberosity causing the humerus to fall over. As with most biological inference concerning general observations on anatomical or morphological features, variation is expected based on behaviour and specific events during life or during ontology.

The life history of each of the specimens included in this study is not known. It should be noted, however, that approximately one quarter of the fox sample was comprised of captive foxes from several fur farms in Canada. Captivity suggests that the natural nutrition, environment and breeding behaviour of these foxes were manipulated by humans. Although the results of the Table Test are still significant for identifying males, it is not known to what extent captivity affected the physiology of these animals. Likewise with domesticated dogs; life history can vary greatly from the lap dog to the racing greyhound. In fact, two of the nine dog humeri that fell over were

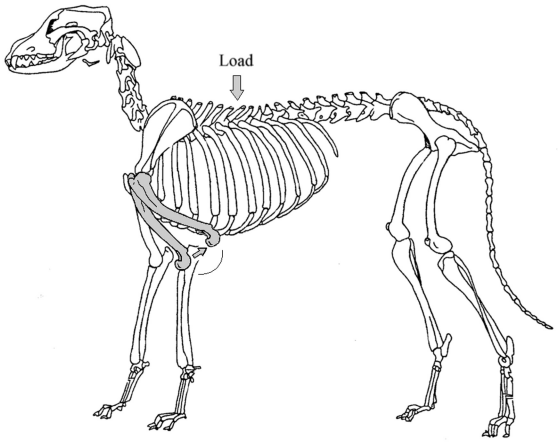


*Fig. 6. Skeleton of a dog showing the position and movement of the humerus in response to loading (skeleton from Davis 1985).*

racing greyhounds, suggesting that a lifetime of conditioning and racing could have resulted in a more developed deltoid, and a change in the normal overall musculature and hence bony attachments in the forelimb. Another consideration is the indirect effects of castration on the skeleton. Domestic dogs, in particular, are neutered or spayed at an early stage of maturity. Although the behavioural affects of this procedure have been studied elsewhere (Hopkins *et al.* 1976), the long term osteological effects of castration of canid males due to behavioural changes is unknown. Castration records were not provided in the modern collections and castration cannot be recognized in archaeological remains in any case. Hence, it is not known how humeri from castrated males or spayed females fare in the Table Test.

## Conclusion

Determining the sex of canids is problematic for a number of reasons. Firstly, diagnostic sexual dimorphic characters in canids are not apparent in the skeleton. Even during life, canids are almost devoid of secondary sexual characteristics compared to other mammals such as suids or cervids. Secondly, human intervention in breeding has resulted into a wide variety of morphology and sizes. Thirdly, the lifeways of domestic dogs are also variable, and the skeletal effects of each life history can be numerous, including the indirect osteological changes due to castration.

Although the Table Test is of limited utility and is not 100% reliable for sexing canids, it can suggest the **likelihood** of the male sex at 85% probability and the female sex at 70% for domestic canids when other sexing information is not available. The test is also applicable to fox, either wild or captive, at 78% probability for identifying male specimens. Six wolf (*Canis lupus*) individuals were tested during the study as well. Although the low number of specimens tested for this species prevents the results from being statistically viable, it may be significant that the Table Test identified the two male humeri (which fell over onto their medial side), and all four female specimens (which rested on their anteroventral side) from the sample – a 100% probability for identifying both sexes. An extended sample of wolf individuals is required to further test the confidence level of the method for sexing wolf specimens. It may be safe to assert, however, that the technique may be more useful to this wild species simply because they exhibit greater size dimorphism within the species compared to fox and dog, and because the species is less likely to have been affected by humans due to their limited association (Fox 1971).

It is fortunate that the test works with the humerus, a sturdy bone which frequently survives intact in the archaeological record. The Table Test is a simple, non-destructive method that can be performed in the field to suggest the sex of an individual canid, where there has been no morphological indication of sex on the post-cranial skeleton of canids in the past. It is hoped that the method will aid in reconstructing preferential selection of sex in domestic canids, enhancing our knowledge of canid/human relationship in historic and even in prehistoric contexts.

*Acknowledgments*

I would like to thank the curators and managers of the osteological collections visited for this project, too numerous to mention here. Their willingness to help and their interest in my research on sexual dimorphism in mammalian skeletons were much appreciated. I am also indebted to Norman MacLeod of the British Museum of Natural History, and Melinda Zeder for suggestions and comments on earlier versions of this paper. I would like to acknowledge the generous funds provided by INSTAP for travel and accommodation at the ICAZ 2002 meetings.

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*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 68–86*

# 5. Sexing Fragmentary Ungulate Acetabulae

*Haskel J. Greenfield*

*One of the problems plaguing zooarchaeological research has been the paucity of easily sexed specimens. Most attempts at sexing specimens have relied upon measurements. In this paper, I will present the results of my research on sexing fragmentary innominates of ungulates. Two features on the medial wall of the acetabular region, the ilio-pubic ridge and medial border of the acetabulum are shaped very differently in males and females. The space between these two features is the medial wall of the acetabular region. In males, the ilio-pubic ridge is dull and poorly visible, and the medial border of the acetabulum is high. In females, the ilio-pubic ridge is sharp and very visible, and the medial border of the acetabulum is low. In females, the wall is short because the pubic bone is thinner (as a result of the need for the pubic joint to maintain flexibility during gestation and birthing). In males, the wall is high and robust because there is no biological function requiring that the pelvic region spread during reproduction. As a result of the conjunction of these features, the wall is high in males and short in females.*

*These features were previously recognized by Grigson (1982) and Prummel and Frisch (1986) for cattle and ovicaprines. In this paper, I will present data to indicate that these patterns can be extended to ungulates as a whole (raw data available upon request). Modern comparative data from a variety of taxa are presented in support of this hypothesis. When such methods are applied to zooarchaeological samples, they dramatically increase the frequency of sexed elements, thereby adding an important new element to interpretations of the data.*

## Introduction

The identification of sexual characteristics in fragmentary faunal remains is of fundamental importance to the analysis of modern and prehistoric zoological assemblages. However, there are few unambiguous sexual characteristics in the mammalian skeleton that unequivocally indicate sex. These are most commonly limited to morphological features such as the presence/absence of suid and equid canines, cervid antlers, carnivore penis bone, etc. (Schmid 1972; Wilson *et al.* 1982).

Since most such characteristics vary in their usefulness for identifying sex between taxa (species, genus, family or higher taxonomic levels), it is often difficult to compare frequencies of different sexes in bone assemblages. Some taxa have clear cut sexual morphological criteria, as mentioned above, but most taxa do not have any diagnostic characters that enable the identification of sex. As a result, some taxa can be better sexed than others based simply upon observation of morphological criteria. This leads to a bias in our ability to compare sexual ratios in assemblages.

Assemblage taphonomy is a major source of bias in the creation and analysis of sexual ratios in bone assemblages. There are a variety of taphonomic factors that can bias the frequencies of sexual bone elements assemblages. First, different bones will have differential levels of resistance to wear from weathering and butchering. For example, teeth are much resistant to attrition from erosion than any post-cranial element. As a result, in highly eroded assemblages, taxa with sexual morphological characteristics in the teeth are more likely to be

sexed than those taxa that do not have such characteristics. The latter taxa would be sexually invisible. A second source of taphonomic bias is the degree of fragmentation of bones with sexually dimorphic characteristics. Many sexual characteristics are found in bones (e.g. baculum) or parts of bones (e.g. pubis) that are extremely fragile. These bones are unlikely to survive the various destructive forces subjected to most assemblages. Other taxa can be sexed from highly resistant bone elements (e.g. equid and suid canines, cervid antlers). Those taxa that could only be sexed based upon the presence of such fragile bones would be more difficult to sex than those with more resistant bone elements. A third source of taphonomic bias might include cultural patterns of butchering and food preparation. Some bones might have a greater chance of being destroyed during butchering and food preparation. In historic faunal collections, with automated butchering machinery, saws often cut through and destroy the joints between limbs. The scapula-humerus and the innominate-femur joint are often destroyed in such methods leading to a bias against taxa that can only be sexed from such elements. A fourth taphonomic bias on bone assemblages is the differential levels of collection and destruction by humans for tool, ornament, or toy production. The bones of different taxa are collected and modified in different ways depending upon their use by humans. For example, the antler of deer might be collected to be used in tool making leading to the inordinate presence of male remains in assemblages, even though both sexes might have been equally exploited for subsistence purposes. All of these can bias the presence or absence of bones with sexual characteristics in bone assemblages (Lyman 1994). As a result, it would be useful to have sexually dimorphic characteristics that cross-cut a wide range of species that would be useful within various levels of taxonomic classification, that are not dependant upon measurements, and that are relatively resistant to the various sources of fragmentation.

In this contribution, I will propose morphological criteria that are both morphologically visible and measurable. Measurement ensures that results are comparable between assemblages and provide confirmation of the morphological observation. Recently collected evidence will be used to demonstrate that the acetabular region of the innominate contains very useful and easily identifiable morphological and metrical features for distinguishing sex in many ungulate taxa. In addition, it will be shown that these features cross-cut individual taxonomic lines and can be traced across a broad swath of the ungulates.

## The sexual morphology of the innominate

The morphology of the innominate is theoretically one of the most sensitive indicators of sex in mammals because of the effects of reproduction upon surrounding osteological structures. A substantial literature exists detailing the sexual characteristics of the innominate in the zooarchaeological and zoological literature (e.g. Boessneck *et al.* 1964; Boessneck 1969; Grigson 1982; Lemppenau 1964; Von Leithner 1927). However, most of the recognized features tend to be on relatively fragile parts of the innominate (e.g. pubic symphysis, proximal end of the ilium, shape of the fossa obturator, etc.). These parts of the innominate tend to be infrequently found in zooarchaeological and palaeontological assemblages. They fuse late in sub-adulthood and are easily destroyed (even after fusion) by a host of attritional processes (Lyman 1994).

Most parts of the innominate do not survive burial because of the relatively high ratio of cancellous to compact bone (Ali and MacLaughlin 1991, 57). One of the most frequently recovered parts of the innominate, however, is the acetabulum and its immediate extensions. The acetabulum fuses relatively early (late in the juvenile phase – Silver 1969; Schmid 1972) and is mostly composed of hard cortical bone. As a result, this region of the innominate has a high probability of surviving most forms of wear.

The most commonly preserved parts of the innominate (in general) and acetabulum (in particular) tend to be the iliac and ischial regions. As an example, the distribution of innominate fragments (and subparts) for *Bos taurus* from the Early Neolithic site of Blagotin is given in Figure 1 (Greenfield and Jongsma n.d.). From a sample of almost 35,000 bone fragments, there are no completely preserved innominates. This is typical of most later prehistoric sites. The most common part of the innominate to be recovered was those parts attached to and including the acetabulum (57.0% of innominate fragments). Of the 53 fragments with acetabulum, the most commonly recovered fragment was the ischium (34.0%). This is followed by acetabulae that included parts of the ilium, ischium and pubis (28.3%). This is followed by a rapid decline in frequency with ilium (13.2%), ilium-ischium (9.4%), ilium-pubis and pubis (5.6%, respectively), and ischium-pubis fragments (3.8%).

The medial face of the iliac and pubic regions of the innominate has several diagnostic features that can be useful for sexing whole or fragmentary specimens. The most commonly noted set of features are the two on the medial wall of the acetabulum where the ilium and pubis join – the ilio-pubic ridge and medial border of the acetabulum (Fig. 2). They are shaped very differently in males and females. In males, the ilio-pubic ridge is dull and poorly visible, and the medial border of the acetabulum is high. In females, the ilio-pubic ridge is sharp and very visible, and the medial border of the acetabulum is low. In females, the medial wall is low because the pubic bone is thinner (as a result of the need for the pubic joint to maintain flexibility during reproduction). In males, the wall is high and robust because there is no biological function requiring that the

| Parts of innominate present | Subparts present | All innominate elements | | With acetabulum attached to part | |
|---|---|---|---|---|---|
| | | No. | % | No. | % |
| Ilium | Acetabulum only | 5 | 5.95% | | |
| | Whole | 1 | 1.19% | | |
| | Acetabulum and body | 1 | 1.19% | | |
| | Body only | 18 | 21.43% | | |
| Ilium Total | | 25 | 29.76% | 7 | 13.21% |
| Ilium, Ischium | Acetabulum only | 3 | 3.57% | | |
| | Acetabulum and body | 2 | 2.38% | | |
| Ilium, Ischium Total | | 5 | 5.95% | 5 | 9.43% |
| Ilium, Ischium, Pubis | Acetabulum only | 14 | 16.67% | | |
| Ilium, Ischium, Pubis Total | | 14 | 16.67% | 15 | 28.30% |
| Ilium, Pubis | Acetabulum only | 2 | 2.38% | | |
| | Acetabulum and body | 1 | 1.19% | | |
| Ilium, Pubis Total | | 3 | 3.57% | 3 | 5.66% |
| Ischium | Acetabulum only | 15 | 17.86% | | |
| | Acetabulum and body | 3 | 3.57% | | |
| | Body only | 6 | 7.14% | | |
| Ischium Total | | 24 | 28.57% | 18 | 33.96% |
| Ischium, Pubis | Acetabulum only | 2 | 2.38% | | |
| Ischium, Pubis Total | | 2 | 2.38% | 2 | 3.77% |
| Pubis | Acetabulum only | 3 | 3.57% | | |
| | Body only | 5 | 5.95% | | |
| Pubis Total | | 8 | 9.52% | 3 | 5.66% |
| Body | | 3 | 3.57% | | |
| Body Total | | 3 | 3.57% | | |
| **Total** | | **84** | **100.00%** | **53** | **100.00%** |

*Fig. 1. Distribution of* Bos taurus *innominate parts (NISP) from Blagotin.*

pelvic region spread. As a result of the conjunction of these features, the wall is high in males and short in females. These features are useful for distinguishing sex especially on fragmentary archaeological material.

This feature has long been recognized in the German literature (Grigson 1982, 10). The earliest citation of this type of is Von Leithner (1927, 36) who describes the pelvic bones as heavier in the male *Bos taurus*. This feature was also used by Lemppenau (1964) who noted that bulls have a thicker medial wall in the acetabulum. This observation was extended to and refined by Boessneck *et al.* (1964, 79–89) in their study of ovicaprines. They observed sexual differences in the medial of the acetabulum.

In the English literature, this feature has a much shorter history. Grigson (1982, 10) observed this characteristic in her analysis of Chillingham cattle and included it in her review of age and sexual criteria for *Bos taurus* (Fig. 2). Prummel and Frisch (1986, 575–576, fig.13) included it in the summary of important distinctions for distinguishing *Ovis aries* from *Capra hircus* (Fig. 3). For ovicaprines, this is not only one of the important features for distinguishing sex, but can be a prelude to the identification of taxon. It is difficult to distinguish between the two taxa without first controlling for sex. Clutton-Brock and Armitage (1990) successfully used acetabulum height to distinguish between sex of Soay sheep.

However, what has been poorly noted in the literature is that the sexual differences in the above feature extend in both directions (cranially and caudally) from the center of the medial wall. As a result, even if only a fragment of the iliac or the pubic areas are preserved, sex can still be distinguished.

1. The thickness of the acetabular wall also affects features on the acetabular end of the ilium, such as the placement of the fossa for the rector femoris. In the *Bovidae*, this fossa tends to be close to the ventral border in females because the medial wall of the acetabular region is thin. In males, the fossa tends to be found nearer the center of the divide between the ventral and dorsal regions because the medial wall of the acetabular region is thick (Fig. 3). Sex can be determined even if only a fragment of the ilium with the fossa for the rector femoris is preserved.

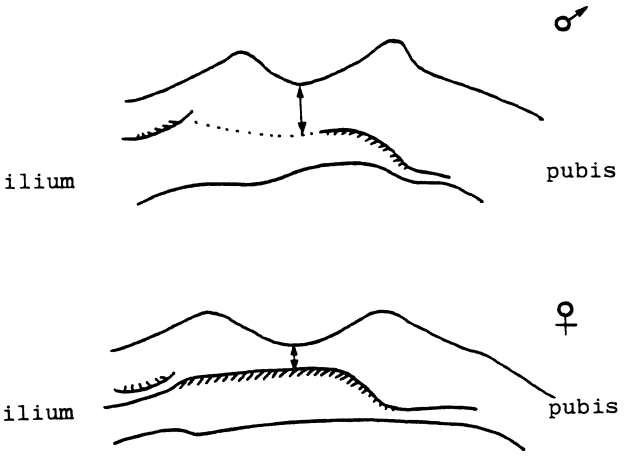


*Fig. 2. Median view of the left acetabular region in* Bos taurus *(Grigson 1982, 8, fig. 1).*

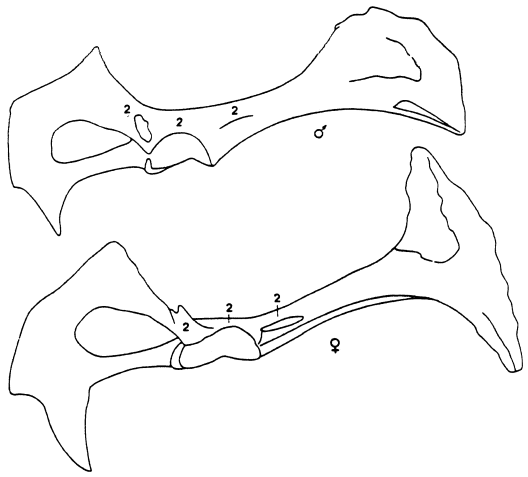


*Fig. 3. Ventral view of the left acetabular region in female and male* Ovis aries *(Prummel and Frisch 1986, fig. 13).*

This feature, however, appears to work in the Bovidae, but not in the *Cervidae* (see below). The large pit-like form of the fossa in the *Cervidae* seems to interrupt the pattern. It takes up too much of the area covering this region of the bone, thereby obscuring any sexual pattern.

**2.** Toward the pubic end of the acetabulum, the pattern is clearer and more consistent. This is because the pubic bone tends to be thinner (or gracile) in females and thicker (or robust) in males. There is a great deal of individual variation, and the differences become more pronounced with age. The result is that even if a fragment of the pubic area is attached to the acetabulum, sex can be distinguished on the basis of the shape and robustness of the bone (see Figs 1 and 7). This pattern has long been noted in the zoological and zooarchaeological literature (e.g. Boessneck *et al.* 1964; Schemnitz 1980; Taber 1956), but rarely utilized. One of the reasons it is rarely utilized in zooarchaeology is that pubic areas of the innominate (or the acetabulum) tend to be more poorly preserved than the iliac and ischial areas.

My initial reason to begin study sex from the perspective of measurements was that there was some variation in the study assemblages. A small number of control museum specimens that might have been identified as male or female on the basis of the thickness of the medial wall and location of the obturator foramen were found to be the opposite sex. In other words, there was not always a clear relationship between sex and morphology in collections of known sex.

The other problem encountered was that the technique and results were difficult to replicate. When demonstrating the feature to students and colleagues, they had difficulty keeping the differences in morphology consistent over time. Part of the problem was population differences within species. But the problem is also affected by degree of fragmentation, which inhibits those with less training and less consistent eye for observation from coming to similar conclusions. As a result, an independent and more objective measure of the feature was necessary in order to be able to control for such observation.

## Measurements

Measurements have long been used as a means to identify the sex of bones in assemblages, especially from taxa or bones that do not have clear sexually dimorphic morphological characteristics (von den Driesch 1976). However, measurements are most useful within well-defined regional populations or within domestic breeds. Spatial, temporal, and sub-specific variation within a species can make it difficult to use measurements to sex osteological material from widely separated regions or time periods. Changes over time and space within a species can blend the metrical differences between sexes. Even though some of the samples contain individuals from potentially different populations (e.g. *Bos taurus, Ovis aries, Capra hircus*), most of the samples come from regionally specific populations (wild animals).

Measurements of the acetabular region of the innominate have long been incorporated into zooarchaeological studiesbecause it is the most commonly found part of the innominate in zooarchaeological assemblages. Duerst (1926) lists several measurements (of which only a few were mentioned) in the most recent compendium of standard measurements (von den Driesch 1976). This is reflected in the measurement to be tested here – the height of acetabular wall. While the measurement for acetabulum height has been long noted in the literature (Duerst 1926), von den Driesch (1976) did not include it

in her survey of animal bone measurements. In fact, von den Driesch was not very optimistic about acetabular measurements, in general. Both the of measures for the length of the acetabulum (LA and LAR) are given a slight relative value by von den Driesch (1976) for the measurement of size estimation ranking. The LA is ranked as a difficult measurement to take, but the LAR as clear and easy to take. There is no information on their value for sexing specimens. This will be tested below.

## Materials

Originally, it was hoped that statistically sufficient sample sizes would be obtainable for each taxon, and for separate populations. This was not possible, though the danger of mixing individuals from different populations is well-known in zooarchaeological analytical methodology. First, while many museums have large collections of remains, few have detailed and accurate information on sex, locality, population, etc. Even fewer have post-cranial remains available for such analyses. Many specimens were inaccurately labeled when compared to museum catalogues.

In the end, only individuals with documented catalogue information that corresponded to the skeletal remains were included in the study. Any questionable specimens were rejected and were excluded from the analysis. The result was that a very small sample of remains from only a few museums were kept and included in the following study.

Measurements were made on a number of adult skeletons of known sex from a number of museum and university comparative collections, including the Agricultural Museum in Budapest (Hungary), Manitoba Museum and the Universities of Manitoba and Winnipeg in Winnipeg (Canada), American Museum of Natural History in New York (USA), and Lund University Zoological Museum (Sweden). Several other museums and collections were visited, but their collections were deemed to be inappropriate for the study due to a variety of problems. Comparative literature is also available from collections in the British Museum of Natural History, London (Clutton-Brock and Armitage 1990). Fig. 4 indicates the number of specimens from each museum. Data were eventually collected on a total of almost 200 specimens, of which 174 are used in this study. Information was gathered for a number of taxa, including *Bison bison* (buffalo/bison), *Bos taurus* (domestic cattle), *Capra hircus* (domestic goat), *Cervus canadensis* (wapiti), *Cervus elaphus* (red deer), *Ovibus moschatus* (muskox), *Odocoileus virginianis* (white-tailed deer), *Ovis aries* (domestic sheep), *Rangifer tarandus* (caribou), and *Sus scrofa dom.* (domestic pig). In addition, a small sample of *Cervus elaphus* measurements was kindly provided by Ola Magnell for a Swedish population. Information was gathered for other taxa as well, but was not included in this study due to extremely small sample. Information on the number of specimens per taxon is found in Fig. 5. The Appendix provides detailed information on each of the specimens.

| **Institution** | **No.** |
|---|---|
| American Museum of Natural History | 78 |
| Hungarian Agricultural Museum | 40 |
| Lund University Zoological Museum | 10 |
| Manitoba Museum | 39 |
| University of Manitoba | 19 |
| University of Winnipeg | 6 |
| **Grand Total** | **192** |

*Fig. 4. Distribution of specimens by institution.*

| | | |
|---|---|---|
| *Bison bonasus* | 1 | |
| *Bos indicus* | 1 | |
| *Bos taurus* | 11 | 11 |
| *Capra hircus* | 20 | 20 |
| *Capreolus capreolus* | 5 | 5 |
| *Cervus canadensis* | 26 | 26 |
| *Cervus elaphus elaphus* | 18 | 18 |
| *Dama dama* | 1 | |
| *Equus caballus* | 2 | 2 |
| *Equus zebra* | 1 | |
| *Homo sapiens* | 3 | |
| *Odocoileus hemionus* | 2 | |
| *Odocoileus virginianus* | 18 | 18 |
| *Ovibus Moschatus* | 6 | 6 |
| *Ovis amnon* | 3 | |
| *Ovis aries* | 25 | 25 |
| *Ovis canadensis* | 1 | |
| *Ovis dallie stonei* | 1 | |
| *Rangifer tarandus* | 7 | 7 |
| *Sus scrofa dom.* | 11 | 11 |
| *Sus scrofa fer.* | 2 | |
| ***Grand Total*** | **192** | **174** |

*Fig. 5. Distribution of specimens by taxon.*

## Methods

In this study, three series of measurements were taken: the height of the medial wall of the acetabulum, length of the acetabulum suggested by von den Driesch (1976), and width of the acetabulum. In addition, the first measurement includes three different versions, reflecting slightly different techniques for holding the callipers in relation to the existing morphology. They are as follows:

*Fig. 6. Photograph of how to place a calliper in order to measure H1.*

*Fig. 7. Photograph of how to place a calliper in order to measure H1 in the interior surface of the acetabulum.*

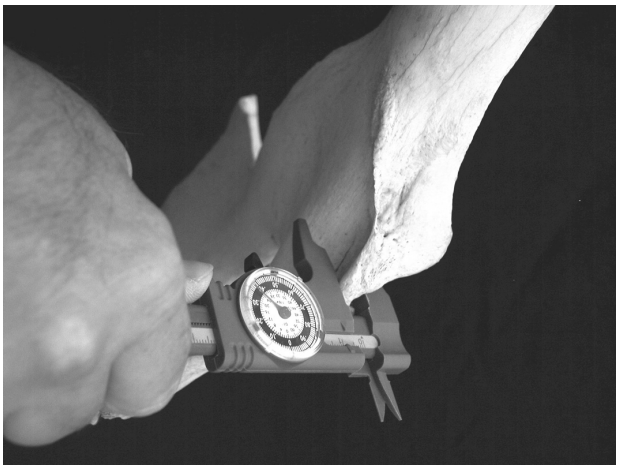

*Fig. 8. Photograph of how to place a calliper in order to measure H1 in the lateral surface of the innominate (behind the acetabulum).*

*Fig. 9. Photograph of the median view of the medial wall of the acetabulum, when a dip or depression is present in the center, of a* Bos taurus.

1. The height of the medial wall of the acetabulum (at the ilio-pubic juncture or H1). The height (or thickness) of the medial wall of the acetabular region can be most accurately and consistently measured by placing the callipers at the line of fusion between the ilium and the pubis (Fig. 6). The measurement should be taken so that the callipers are held parallel to the medial wall of the acetabular region. The most replicable position to take this measurement is when the points of the callipers are placed above and below the center pit of the acetabulum (Fig. 7). The aim is to have one side of the callipers leaning on and over the inner lip of the acetabulum with the point of the calliper touching the bottom of the acetabular pit, while the other arm should press against the medial face of the acetabulum (Fig. 8). A problem with this measurement is that a variable morphological feature appears in the female of some taxa (e.g. *Bos taurus*). The medial wall of the acetabulum is sometimes not smooth. Occasionally, it is characterized by a dip or depression in the center (Fig. 9). When this feature appears, it becomes more difficult to measure the height of the acetabular wall. The measurement thus includes the dip.

2. H2 is a second version of the height of the medial wall of the acetabulum. This measurement was taken in a more traditional manner. The tips of the calliper arms are placed at the ventral and dorsal edges of the acetabular lip. It would seem to be the most logical measure of the

feature, but was found to be inconsistently taken by several people. This is an especially problematic measurement on males where there are not any fixed points from which to measure (see Fig. 1). Hence, errors can easily creep into the analysis.

3. Length of the Acetabulum. The two most commonly used measurements of the acetabulum (LA and LAR) are measured (Fig. 10). The technique used for these measurements is described in von den Driesch (1976). The bone features necessary for the LA and LAR measurements are found on the lateral side of the acetabulum. This side appears to be denser and preserves more commonly than the medial side. Hence, it is possible to measure them more frequently than on the medial side of the acetabulum.

4. Width of acetabulum (WA). The width measurement is less commonly used because it requires both the pubic and ischial sides of the acetabulum to be present, something which is much less common since the connection is more fragile. However, it is still used in the literature as a means of establishing sex (West 1990). Measurements are also provided for it.

5. Distance of the fossa for rector femoris to medial and lateral edge. The location of this fossa can be used as an indicator of sex in bovids. It appears to lie closer to the medial edge in females than males (see Fig. 9). Measurements from the center (or deepest) point of the fossa to the medial and lateral edges were noted.

## Results

Since size is often used as a proxy measure for sex, the distributions should approximate sexual dimorphism. The results, however, are not so clear. The results will be discussed measure by measure.

### *Height of the acetablum (H1) – Fig. 14 in Appendix*

The original hypothesis was that the height of the medial wall of the acetabular region would be consistently high in males and low in females for many species of the bovid and cervid families in the modern control specimens. The results are, however, not so unambiguous.

The bovid family yielded the clearest results. They yielded consistently different and nonoverlapping ranges for males and females. The taxa with the clearest separation include *Bison bison* (Fig. 14a), *Bos taurus* (Fig. 14b), *Capra hircus* (Fig. 14c), and *Ovibus moschatus* (Fig. 14g). Regardless of breed or geographical distribution, the sexes are clearly differentiated by this measurement. This is true for sub-adults in the sample, as well. These individuals already have the sexually differentiated characteristics and fall into the measurement distribution for their sex (e.g. *Ovis aries*). Some of the samples were small (e.g. *Ovibus moschatus*), resulting in the suspicion that the clear results are due to small sample size effects. But the separation of the two sexes is relatively clear and is expected to be confirmed as larger samples are gathered. The results of the small *Sus scrofa dom.* sample also indicate that the measurement can be used to separate the two sexes (Fig. 14j). Females tend to be smaller than males. Some problems were found in the analysis of the H1 measurements. The first problem was with the *Ovis aries* sample. A single supposedly female specimen was found at the lower end of the male spectrum (Fig. 14h). The problem could be that this specimen was incorrectly identified as a female. There was no information listed in the catalogue, but sex was marked on the box that contained the specimen. If this specimen was removed from the analysis, the separation would be clearer.

The problem of overlap between the sexes is found throughout are the cervid family. There is some overlap in the *Cervus canadensis* sample between female and males, but it is only at the lower end of the range (Fig. 14d). The overlap is more pronounced with the *Cervus elaphus* sample, because a single large female is found at the upper end of the size range (Fig. 14e). Part of the problem with this sample is that it includes specimens from the Manitoba population (including the really large female), while the rest of the females derive from the Hungarian population. A similar situation exists for the *Cervus canadensis* sample. There is a single large female that comes from the American Museum of Natural History (AMNH) collection, but there was no any information on its original locality. The range of overlap is also considerable for *Odocoileus virginianus* sample (Fig. 14f). At the lower end of the size distribution, males and females overlap. This may also be a population mixing problem since the sample included populations from eastern and northern North America (those from the AMNH and Manitoba collections). Nonetheless, among cervids as a whole, most of the females fell at the lower end and most of the males fell at the upper end of the distribution. The problem is largely with those toward the middle range.

The problem of mixing populations is reflected by the *Cervus elaphus* data from the Zoological Museum in Lund. The specimens are from the same area, Scania, the most Southern part of Sweden and were collected during the period 1959–1971 (Ola Magnell, pers. comm. 2002). In Fig. 14e, the Swedish (L) and Hungarian (H) populations are distinguished. Two interesting observations can be made from these data. First, the Swedish population falls into the same range as the Hungarian specimens, even though they are geographically separated populations. Second, there is no overlap in the measurements of the height of the medial wall of the acetabulum between females and males, except for a single very large (immature) female. However, the measurement is from

an unfused acetabulum. It either means that some overlap may occur in size, there was some mixing of populations, there was an error in the catalogue, or that the height of the medial wall may thin as females fuse. At this point, it is difficult to resolve this issue. According to Magnell's observations on the Swedish sample, the acetabulum is thicker by the symphysis between the ilium and pubis on unfused coxae than on acetabulum from fused individuals (pers. comm.). However, this remains to be systematically demonstrated.

The issue of castrates for domesticates needs to be addressed. It is well known that castration can also influence measurements. Since the bones of castrates continue to grow longer than those of uncastrated males, the bones of castrates tend to be longer and slimmer. Castrated males typically fall into the size range of females, in terms of slenderness, but achieve the lengths of normal males (Davis 1996, 2000; Payne and Bull 1982). However, the degree of affect depends upon when the castration took place. Early castration has a more significant effect upon measurements because this is the period of rapid bone growth and development and allows for a longer period of growth (Davis 2000). In contrast, later castration has little effect since most of the major bone growth is already completed. Unfortunately, there were no clearly identified castrates in the sample examined here. None of the museum samples clearly indicated whether they were from castrates. Some of the males appear to be very gracile and may derive from castrates, but these specimens seem to follow the pattern of males. Nonetheless, it is expected that castration will have little effect upon the features discussed here since sexually diagnostic features have less of an effect on bone length, but with the height of the medial wall. Larger and better control samples are necessary to ensure that the timing of castration does not affect the height of the medial wall.

### *Height of medial wall of acetabulum 2 (H2) – Fig. 15 in Appendix*

Analysis of the distribution of the H2 measurement yielded a less than satisfactory result. In almost all cases, there was some overlap between the male and female distributions (*Bison bison, Bos taurus, Capra hircus, Odocoileus virginianus Ovis aries, Rangifer tarandus, Sus scrofa dom.*). Only the small sample of *Ovibus moschatus* did not exhibit any overlap (Fig. 15f). Surprisingly, given the results of the H1 analysis, the only taxon that did not have an overlap between males and females was *Cervus canadensis* (Fig. 15d). None were available for the *Cervus elaphus* sample, unfortunately. In general, it is felt that this measure did not yield adequate results because it was difficult to consistently measure this measurement. In contrast to H1, there were no morphological features that could be consistently identified and taken as a basis for the measurement.

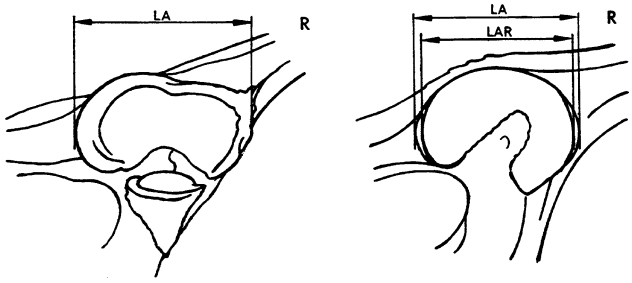


*Fig. 10. Illustration of the LA and LAR measures (von den Driesch 1976, figs. 34c and 34d) and width of acetabulum measures. Left is a* Bos *acetabulum and right is a* Equus *acetabulum.*

### *Length of acetabulum (LA and LAR) – Fig.s 16 and 17 in Appendix*

The length of the acetabulum (LA) is the most commonly taken measurement of the acetabulum. Even so, it is described as being of relatively poor value for reconstructing size (and hence sexing – von den Driesch 1976, 7, 83). The length of acetabulum rim (LAR), in contrast, is supposedly a better measure. However, the data from this study indicate otherwise.

Any number of histograms showing the distribution of LA and LAR measures for each of the taxa studied show significant overlap in the distribution of the two sexes. In other words, they are poor measures for distinguishing sex in each of the bovids (e.g. *Bison bison, Bos taurus, Capra hircus, Ovis aries* – Figs 16a, b, c, h and Figs 17a, b, c, h) and cervids (*Cervus canadensis, Odocoileus virginianus*, *Rangifer tarandus* – Figs 16d, f, i and Figs 17d, f, i).

In one of the small samples (*Ovibus moschatus* – Fig. 16g and Fig. 17g), these measurements appear to distinguish between the sexes. But this may reflect the vagaries of small sample size. Probably, a more important reason that these are such poor measures is that the ischial lip edge of the acetabulum is notoriously difficult to isolate, and measurements based on it are difficult to replicate.

Another problem is these two measurements strongly covary in the modern comparative samples. One is a predictor of the other (the *r* relationship). The correlation coefficient of LA against LAR was very high for each of the taxa, showing they are codependent measures (Fig. 11). The very high $r^2$ coefficient between these two variables indicates the level of probability of the relationship. In contrast, the *r* correlation coefficient between the height of the medial wall of the acetabular region and the LA indicates a much lower level relationship. The vastly lower $r^2$ indicates the low level of probability of the relationship. This follows the results of the above analysis that indicates that each of these measures is not an equally good predictor of sex. Overall, each of the

| | LA:LAR | | Height:LA | |
|---|---|---|---|---|
| **Taxon** | ***r*** | ***r2*** | ***r*** | ***r2*** |
| *Bos taurus* | 0.9749987 | 0.9506225 | 0.7390173 | 0.5461466 |
| *Bison bison* | 0.9741713 | 0.9490098 | 0.8606998 | 0.7408042 |
| *Capra hircus* | 0.9718988 | 0.9445873 | 0.8356925 | 0.698382 |
| *Cervus canadensis* | 0.9653772 | 0.9319532 | 0.6887795 | 0.4744171 |
| *Cervus elaphus* | 0.9882627 | 0.9766632 | 0.8326914 | 0.6933749 |
| *Odocoileus virginianus* | 0.9736591 | 0.948012 | 0.7368461 | 0.5429422 |
| *Ovis moschatus* | 0.9884668 | 0.9770666 | 0.8417071 | 0.7084708 |
| *Ovis aries* | 0.9647032 | 0.9306524 | 0.749204 | 0.5613067 |
| *Rangifer tarandus* | 0.9858914 | 0.9719819 | 0.6246261 | 0.3901577 |

*Fig. 11. Pearson's* r *correlation coefficients for the relationship between the LA and LAR measures.*

measures can suggest sex to varying extents, but the height of the medial wall is the more sensitive measure.

### *Width of acetabulum (WA) – Fig.18 in Appendix*

When the width of the acetabulum is considered, the results are more consistent. Males tend to be larger than females, but there is significant overlap in the center of the range for most taxa for both bovids and cervids (Fig. 18a, b, d, e, f, g, h – *Bison bison, Bos taurus, Cervus canadensis, Odocoileus virginianus, Ovibus moschatus, Ovis aries, Rangifer tarandus*). The resulting impression of these traditional measures is that there is little utility in this measurement in order to distinguish sex. Some taxa (e.g. *Capra hircus)* and sample sizes are smaller for this measure since it was added later in the study.

### *Distance of rector femoris fossa to medial and lateral edge of ilium – Fig. 19 in Appendix*

The last measure to be discussed is the distance of the fossa for the rector femoris to medial and lateral edge of the ilium. Unfortunately, this measure was not included in the early stages of the analysis and there are only insufficient samples sizes to be discussed at this point. At present, it can be said that the same problem that exists for the height of the ilium also plagues this measurement – it works for bovids but not necessarily for cervids.

A good bovid example is the *Ovibus moschatus*. It has the best data to demonstrate that the distance from the center of the fossa to the ventral edge can be used as a predictor of sex (Fig. 19e). There is no evidence of overlap between the sexes. In contrast, *Rangifer tarandus* can be used as a good example of the problem that arises with cervids; once again, there is overlap in the lower end of the range (Fig. 19f).

### *A zooarchaeological sample – Fig. 20 in Appendix*

The usefulness of this type of data is apparent when it is applied to a zooarchaeological assemblage. The Early Neolithic settlement at Foeni-Salaş in southwestern Romania was excavated and analyzed by the author in 1992–94 (Greenfield n.d.). Large quantities of domesticated fauna were found in fragmentary condition, and none preserved clearly identifiable bone elements with diagnostic sexual morphologies. Among the Early Neolithic faunal remains, five acetabular regions of domesticated cattle innominates were uncovered and which were measured with the H1 measurement (Fig. 20a). An additional measurement from an Early Iron Age deposit at the site was also included for comparison.

Based upon the measurement of the height of the medial wall of the acetabular region, it would appear that there were two size groups – potentially, one male and five females. This is borne out by the metrical observation of the morphological characteristics described above. It is likely that only the individual with a measurement of 19.5mm would have been a male, given the large separation in size. This is supported when the data from Foeni-Salaş and from the comparative collections are plotted on the same histogram (Fig. 20b). While the separation of sex was clear with the Foeni-Salaş data alone, the situation is less clear when plotted with the comparative data. Combining the Foeni-Salaş measurements with those of modern cattle is not necessarily a valid comparison, but useful for illustration. The animals are from different populations and, as a result, statures. It is clear that the Early Neolithic cattle from Foeni-Salaş are larger than the modern samples.

The implication is that among the adults, mostly females are being slaughtered. In contrast, most males were probably slaughtered as immature animals. This is supported by the data in Fig. 12, which present information on the distribution of sex of innominates identified on the basis of morphology of the pubic-iliac regions. It clearly shows that all females were adults (on the basis of fusion and muscle markings). The males were divided

| Measurement (mm) | Period | Sex based on morphology |
|---|---|---|
| 11.5 | EN | Female |
| 19.5 | EN | Male |
| 12.5 | EN | Female |
| 12 | EN | Female |
| 9.5 | EN | Female |
| 8.5 | EIA | Female |

*Fig. 12.* Bos taurus *innominate measurements from Foeni-Salaş.*

between the subadults and adults. Among the specimens that could not be sexed because the region was not present, the distribution also included juveniles. Hence, models of exploitation strategies that emphasize keeping alive as many animals (e.g. Redding 1984) as possible would appear to be invalid in this case. It is interesting to observe that the single Early Iron Age female specimen fell within the size range of the Early Neolithic females.

A testimony to the utility of the H1 measure was that it was the most frequently measured innominate specimen in the sample. It was possible to measure the LA or LAR in only a single case, another indication of the limits of these measures. It would not have been possible to otherwise identify the sex of any of the specimens without the use of the H1 measurement and the observation of morphological features. The traditionally used sexual indicators were not present in any of the specimens.

Fig. 13 provides comparable information on the distribution of sex for other major taxa from the Early Neolithic at the site. Analysis of these data further demonstrates the utility of sexing with these features.

## Conclusions

This study began as a result of personal experiences (mostly frustration) in sexing fragmentary animal bones from archaeological sites. This frustration has been widely experienced in the discipline. Most fragments that can be sexed do not appear with regularity in most assemblages. As a result, it was with great relief to learn that both Grigson (1982) and Prummel and Frisch (1986) concurred that acetabuli could be sexed based upon morphology. This is one of the more common elements in assemblages because of the density of the bone.

However, even after the publication of their results, most zooarchaeologists that I have spoken with have ignored (or forgotten about) the shape of the acetabulum as an indicator of sex. It was implicitly assumed that since it fuses early, it would not be a reflection of the hormonal changes in the body that begin to take place at the onset of sub-adulthood. However, this is the not case; sexual dimorphism is visible in the shape of the acetabulum. The question became to what extent could their differences be recognized and if they could be verified.

In this study, I have attempted to verify and extend their results. While sexual differences in the shape of the features along the medial surface of the acetabular region are visible (Grigson 1982; Prummel and Frisch 1986), it is also possible to quantify the size relationship between the sexes and thereby remove any subjectivity in identification of sex. While the height of the wall of the acetabular region has long been applied in sexing some taxa (i.e. *Bos taurus* and Caprinae), it has been found in this study to be equally useful for sexing a host of other species in the same family (Bovidae). It can be extended to other closely related families (e.g. Cervidae), but with some caution. Most importantly, measurements of the height of the acetabular wall can be collected, compared with modern and ancient samples, and used to identify sex. It is the type of sexual identifier that would be useful across different taxa, and especially for those that are commonly found in palaeontological and zooarchaeological assemblages (as long as population is held as a constant). The height of the medial wall of the acetabulum also affects the surrounding medial walls of the iliac and pubic regions of the acetabulum. As a result, it becomes possible to sex acetabular fragments with only these parts still attached. Sexing acetabuli with this constellation of features becomes possible on a larger scale than before. This is a very useful feature for identifying the sex of even fragmentary pelvic fragments because only a part of the length of the wall needs to be preserved in order to see the pattern. The pattern begins in the pubic bones and continues into the iliac region of the innominate.

It was also discovered that the ability of more traditional measurements of the acetabular region to distinguish between the sex, LA and LAR (von den Driesch 1976), was quite disappointing. Histograms of these two measurements indicate that they are relatively insensitive to sex. The height of the medial wall of the acetabulum was a better indicator of sex than the length (LA and LAR) and width (WA) measures. This is true even for cervids (e.g. *Cervus elaphus*).

This study has shown that a number of closely-related families within the order Artiodactyla share the sexual morphological characteristics of the innominate. To date, it has been identified among the Cervidae and Bovidae. Some differences were also observed in the Suidae, and it is expected that these will be born out by further observations. The differences may also be present among the other families of the order (Tayassuidae, Hippopotamidae, Camelidae, Tragulidae and Giraffidae), but this remains to be tested. Modern comparative data from a variety of Bovidae and Cervidae taxa are presented in support of this hypothesis. When such methods are applied to zooarchaeological samples, they dramatically increase the frequency of sexed elements, thereby adding an important new element to interpretations of the data.

| Taxon | Age | Sex (no.) | | | | | Total |
|---|---|---|---|---|---|---|---|
| | | Female | Female? | Male | Male? | Unknown | No. |
| *Bos taurus* | Juvenile | | | | | 2 | 2 |
| | Subadult | | | 1 | | 8 | 9 |
| | Subadult/Adult | | | 2 | 1 | 6 | 9 |
| | Adult | 9 | | 1 | | 8 | 18 |
| | Unknown | | | | | 1 | 1 |
| | Total | | | 4 | 1 | 25 | 39 |
| *Capra hircus* | Subadult | | | 1 | | | 1 |
| | Adult | 2 | | 1 | | | 3 |
| | Total | 2 | | 2 | | | 4 |
| *Ovis aries* | Juvenile | | | | | 1 | 1 |
| | Subadult | | | 3 | | 1 | 4 |
| | Subadult/Adult | 4 | 1 | | | 3 | 8 |
| | Adult | 3 | | | 1 | | 4 |
| | Total | 7 | 1 | 3 | 1 | 5 | 17 |
| *Ovis/Capra* | Infantile | | | 1 | | | 1 |
| | Juvenile | | | 4 | | 1 | 5 |
| | Subadult | 2 | | 2 | | 4 | 8 |
| | Subadult/Adult | 2 | | 4 | | 11 | 17 |
| | Adult | | | | | 1 | 1 |
| | Unknown | 1 | | | | | 1 |
| | Total | 5 | | 11 | | 17 | 33 |
| *Capreolus capreolus* | Subadult | | | | | 2 | 2 |
| | Subadult/Adult | | | | | 1 | 1 |
| | Adult | | | 1 | | | 1 |
| | Total | | | | | 3 | 3 |
| *Cervus elaphus* | Subadult/Adult | 1 | | | | | 1 |
| | Adult | | | 1 | 1 | 1 | 3 |
| | Total | 1 | | 1 | 1 | 1 | 4 |
| *Sus scrofa fer.* | Adult | | | | 1 | | 1 |
| | Total | | | | 1 | | 1 |

*Fig. 13. Distribution of innominates by sex in the Early Neolithic deposits of Foeni-Salaş.*

Can the characteristic (height of the medial wall of the acetabulum) be extended to other infraorders within the order of Ungulata (hoofed mammals), such as equids? I have not had the opportunity to apply the characteristic in a systematic manner to the order Perissodactyla, although it may be possible in the future. However, I expect that such differences will also be present given the visible sexual dimorphism. The same may also be true for other orders, such as the Carnivora. However, sufficient numbers of sexed individuals were difficult to come by and will need further investigation. Other areas for further investigation include the study of the effects of castration and states of fusion on the morphology of the ilio-pubic symphysis and neighboring regions.

In sum, the near exclusive reliance of most of the zooarchaeological community upon the limited set of measurements proposed in von den Driesch (1976) was not her original intention. She should be applauded for her creation of a compendium of the more useful measurements which could be then used in a standardized manner and be easily taught to the rapidly growing population of young analysts (many of whom never consulted such literature). As she noted in her introduction, the measurements she proposed for inclusion are only those that were most commonly utilized at the time and found to be most useful. However, she never meant to close off the addition of new or inclusion of older measurements. Analysis of the more commonly used measurement distributions (LA, LAR, and WA) do not clearly reflect sexual differences and it would seem to use these measures on bones from zooarchaeological samples in order to distinguish sex. Other more sensitive measures need to be included as well.

*Acknowledgements*
I would like to acknowledge the help of the many

colleagues who contributed to my research – Laszlo Bartosiewicz (Budapest), Janice Klapecki (Manitoba Museum), Ross McPhee (American Museum of Natural History), Ola Magnell (Lund, Sweden), and Tina Jongsma and Kate Peach. The measurements in Budapest were taken in September 1993, the American Museum of Natural History in December 2000, Manitoba Museum in July 2002, and the Universities of Manitoba and University of Winnipeg in 1999. Without their unstinting aid and willingness to share data, this project could never have been accomplished. Any error is my fault, alone. I am grateful to the Institute for Aegean Prehistory for the grant which aided travel to Durham for the ICAZ 2002 conference.

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# Appendix

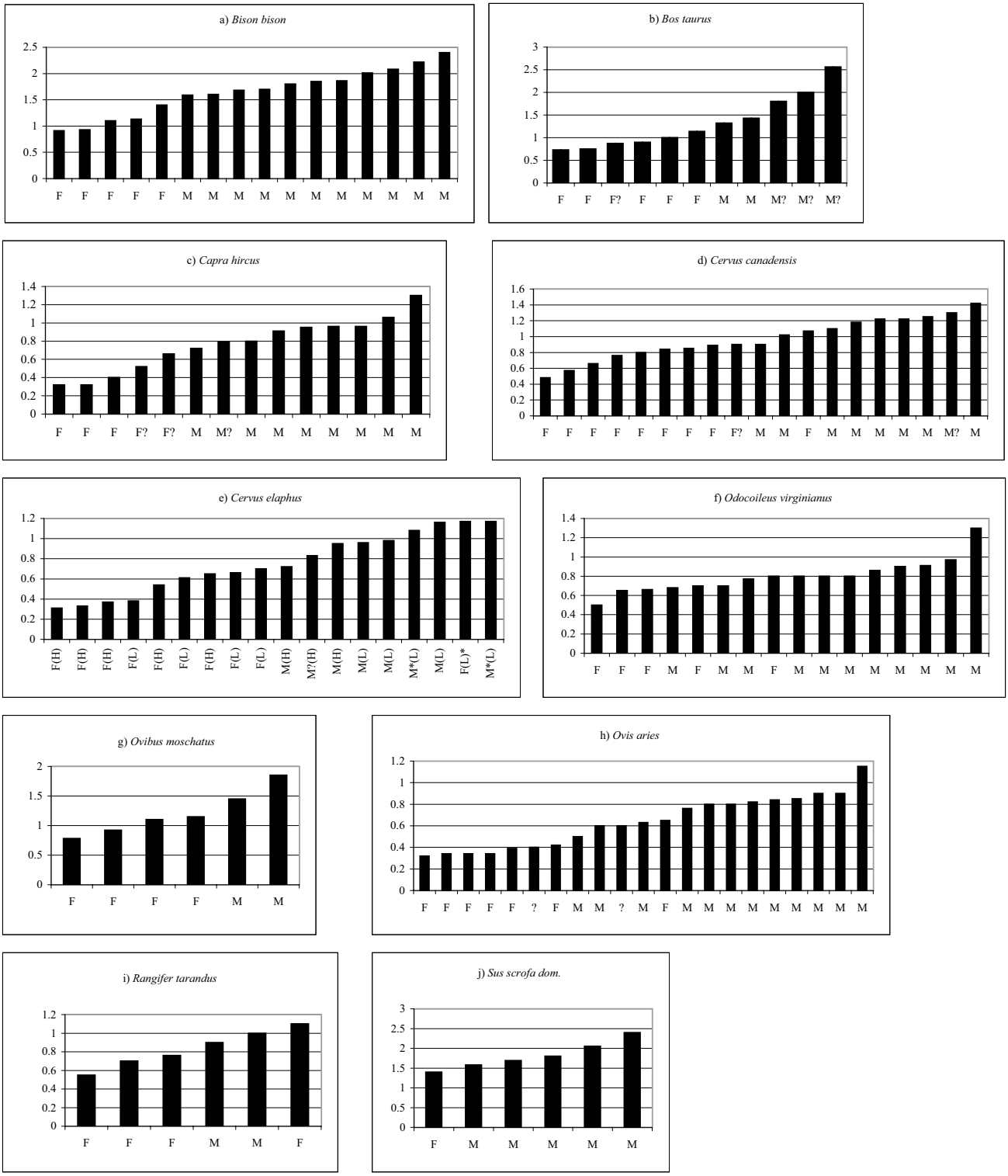


*Fig. 14. Histogram of distribution of the measurement of the height (H1) of the medial wall of the acetabulum for a variety of taxa. The x-axis represents sex and the y-axis represents the measurement in cm. The symbol * indicates an unfused specimen, (L) indicates Lund, Sweden, and (H) indicates Hungary. The taxa are presented in alphabetic order.*

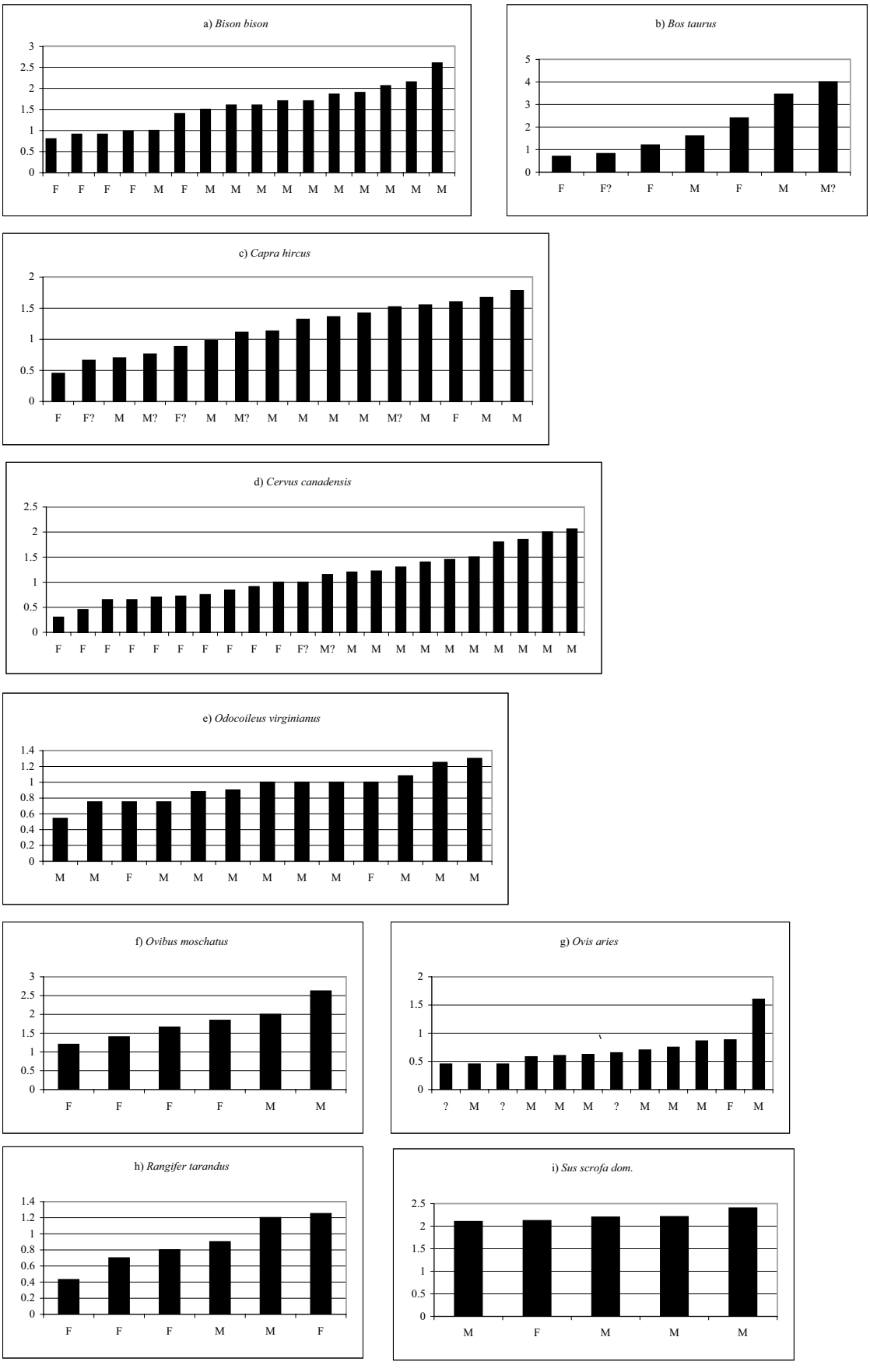


*Fig. 15. Histogram of distribution of the H2 measurement of the medial wall of the acetabulum for applicable taxa.*

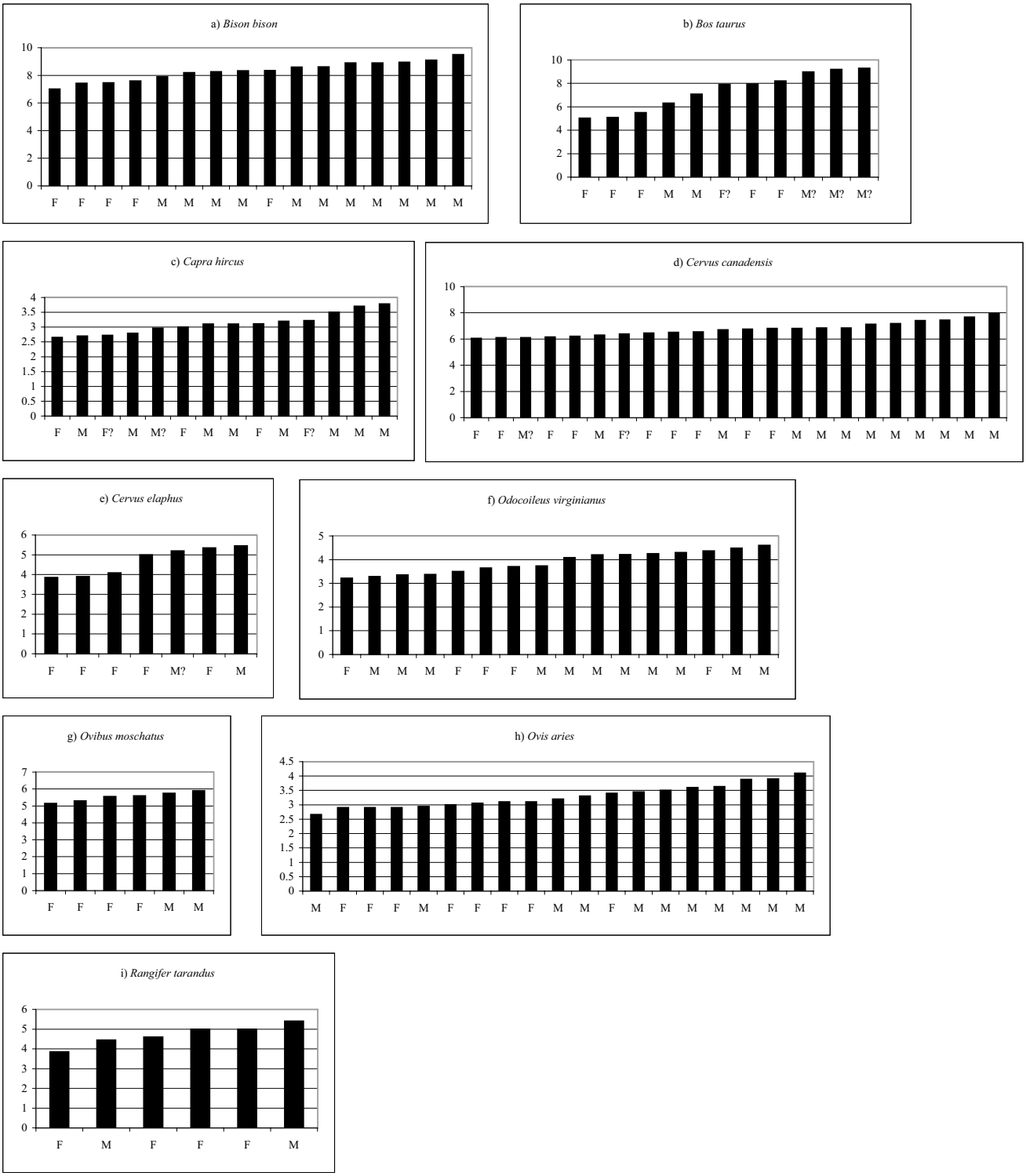


*Fig. 16. Histogram of distribution of the LA measurement of the acetabulum for applicable taxa.*

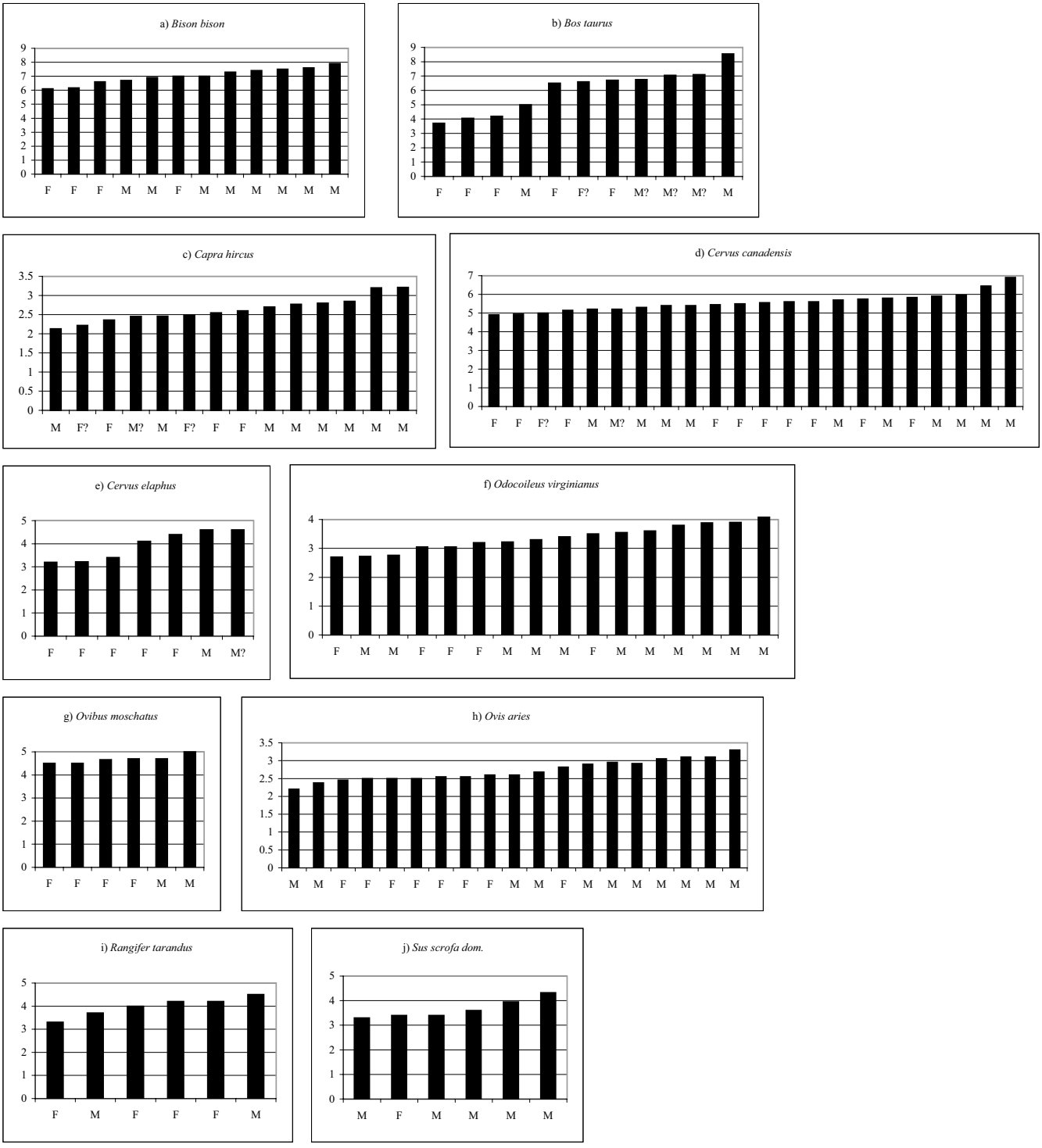


*Fig. 17. Histogram of distribution of the LAR measurement of the acetabulum for applicable taxa.*

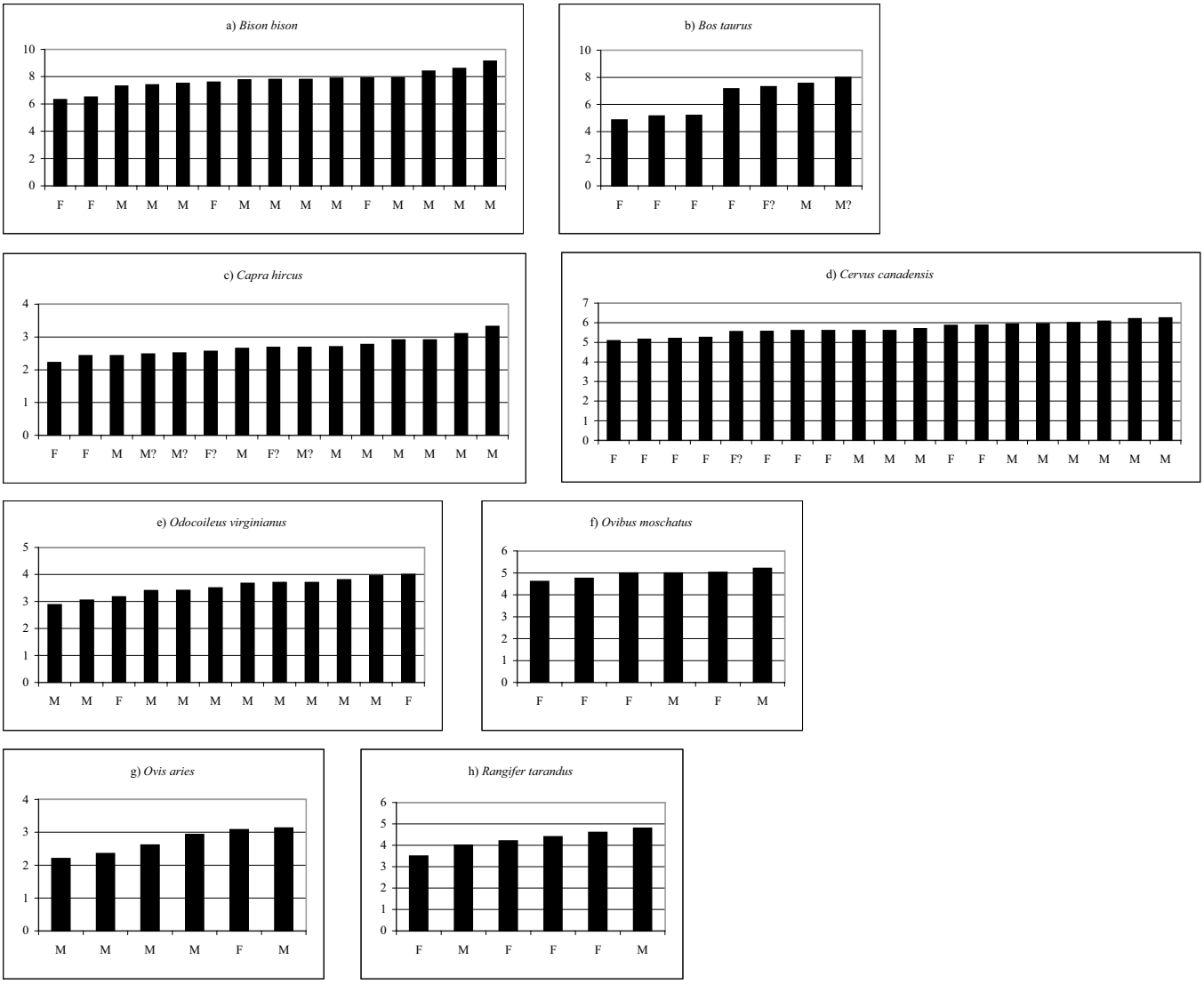


*Fig. 18. Histogram of distribution of the width measurement of the acetabulum for applicable taxa.*

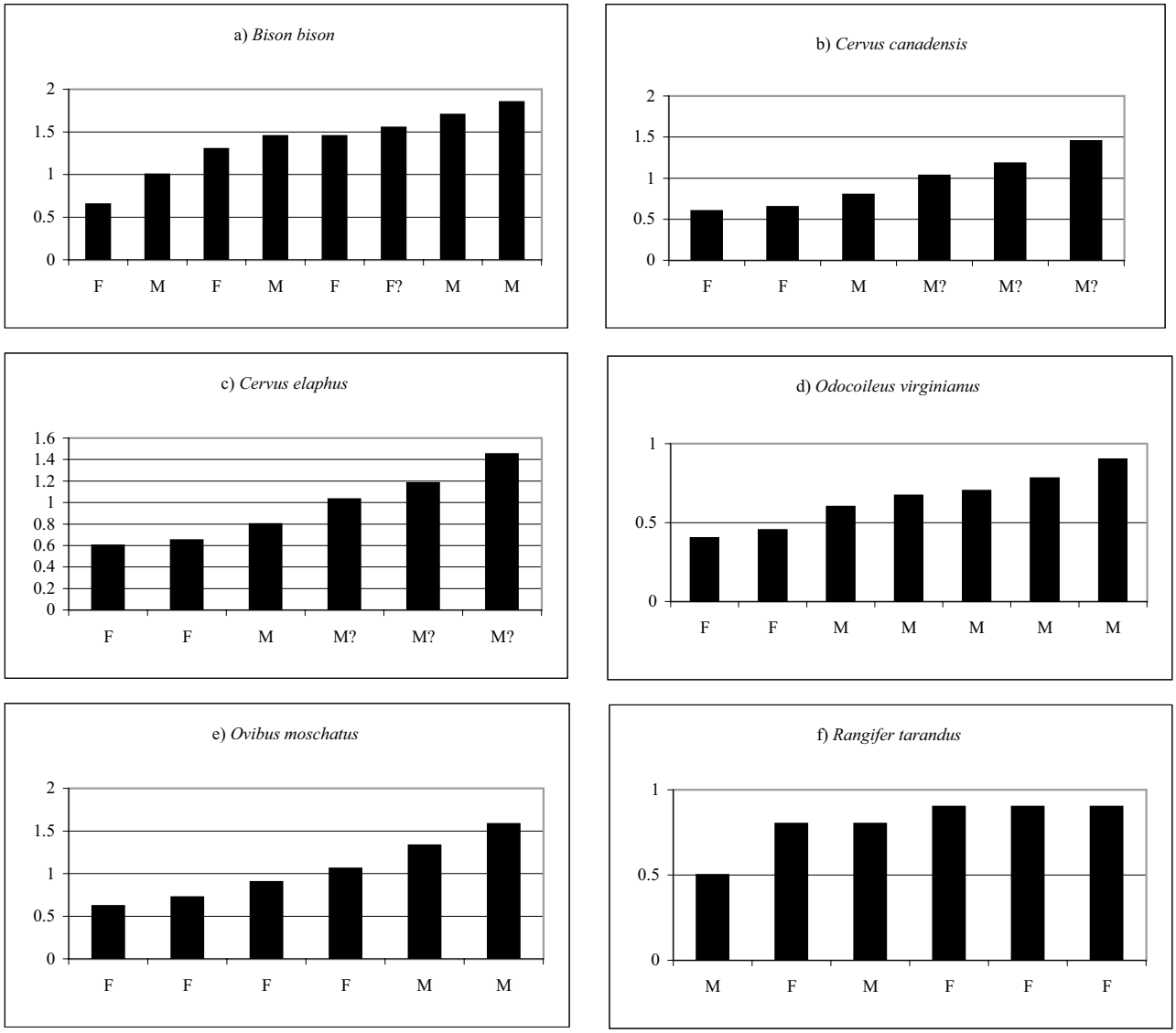


*Fig. 19. Histogram of distance from ventral edge of ilium to center of rector femoris (measured from middle of fossa or deepest point) for applicable taxa.*

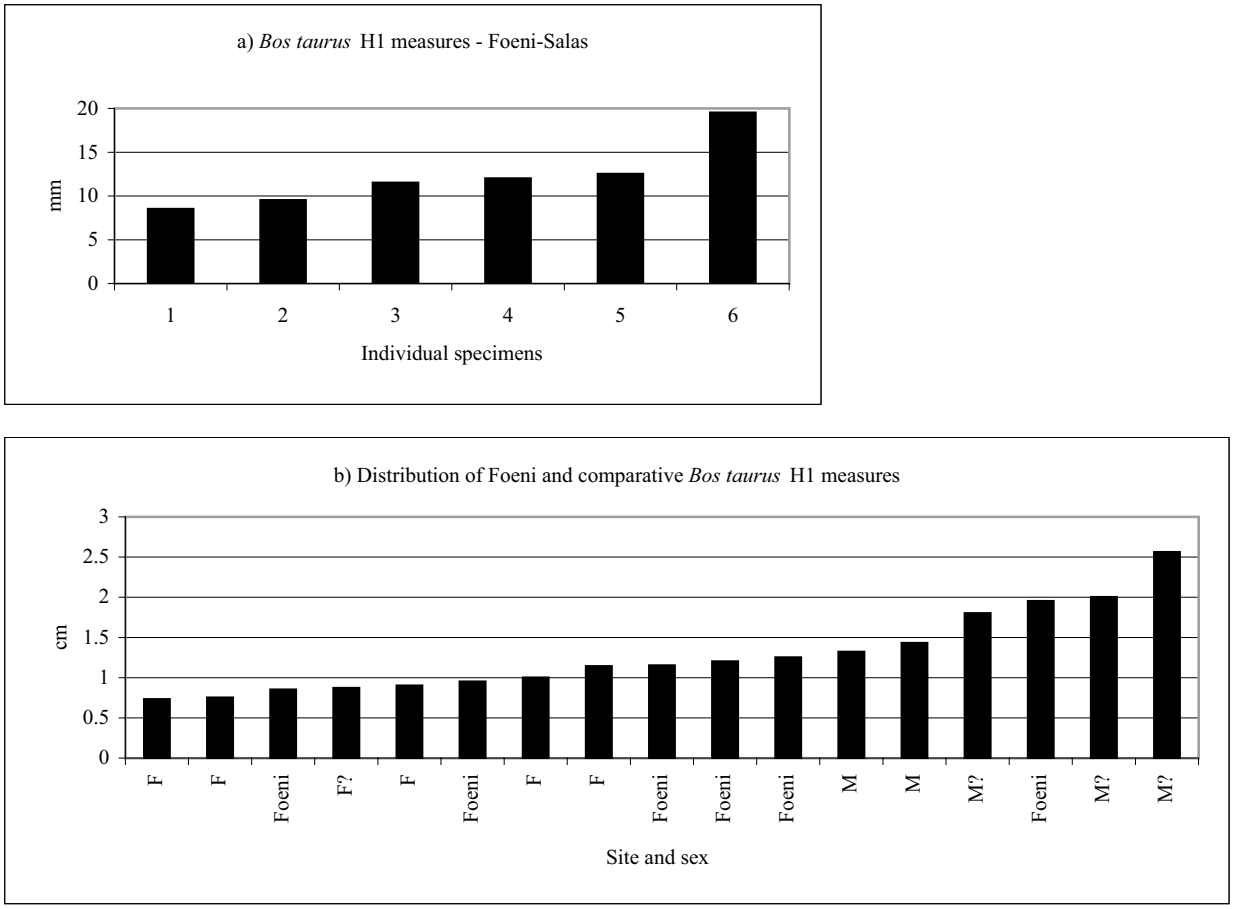


*Fig. 20. Modern and ancient* Bos taurus *specimens compared. a) Distribution of* Bos taurus *H1 measures (mm) from Foeni-Salaş. b) Comparison of the distribution of* Bos taurus *H1 measures from Foeni-Salaş and modern comparative collections.*

*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 87–118*

# 6. Reconciling Rates of Long Bone Fusion and Tooth Eruption and Wear in Sheep (*Ovis*) and Goat (*Capra*)

*Melinda A. Zeder*

*Age determination by long bone fusion and tooth eruption and wear patterns are methods used by zooarchaeologists around the world to build mortality profiles of archaeofaunas. These profiles, in turn, are used to reconstruct hunting and herding strategies fundamental to understanding the lifeways of people of the past. However, the empirical grounding for these techniques is shaky at best. Base-line studies rates of long bone fusion and tooth eruption and wear in caprines are generally based on known age populations of domestic breeds of sheep and goats that may not be an entirely appropriate model of ancient wild and early domestic animals. In this study, a large collection of mostly wild modern sheep and goats from Iran and Iraq is examined with the aim of addressing a number of core questions about the comparability of these methods for constructing mortality profiles in ancient caprines. The study helps to resolve open questions about the sequence and timing of epiphyseal long bone fusion in sheep and goats, and both confirms and refines widely used tooth eruption and wear sequences. It also finds systematic differences in the reconciliation of fusion and dental based aging sequences between sheep and goats and males and females that are likely related to differences in the rate of tooth attrition.*

## Introduction

The reconstruction of mortality profiles of animal remains from archaeological sites is a fundamental tool in zooarchaeological analysis. Sheep and goat mortality profiles, in particular, play a central role in the examination of a wide range of problems, ranging from the transition from hunting to herding to the development of specialized pastoral economies. As a result there is a special premium placed trying to achieve the greatest amount of verisimilitude possible when developing methods for the reconstruction of caprine mortality profiles. The literature is replete with studies aimed at providing a firm empirical basis for fixing age at death of sheep and goat from remains they leave behind in archaeological sites, whether they be teeth or post-cranial bones. For years zooarchaeologists have been peering into the mouths of living sheep and goats, rummaging through out-of-the-way collections of modern caprine skeletons, even scouring obscure 18th century records to determine the precise sequence and timing of long bone fusion and tooth eruption and wear in order to provide a more accurate standard for the reconstruction of mortality profiles of ancient sheep and goats.

This study represents one more contribution to this general effort. Like other studies of this nature it is based on a large collection of modern skeletal remains of sheep and goats. Unlike earlier work that used skeletal material from domestic breeds or so called feral animals of domestic ancestry, this study focuses on a collection comprised primarily of wild animals from Iran and Iraq, the general region where initial domestication of these animals took place. As a result, this unique collection offers information on the sequence of bone fusion and the patterns of tooth eruption and wear in caprines closer to their natural state, before the development of genetically improved breeds raised under conditions far removed from those of ancient wild and domestic sheep and goats. Specific questions asked of this collection are: 1. What is the sequence of long bone fusion in these wild caprines, are there systematic differences between sheep and goat

fusion patterns, and how do the patterns derived for this study compare with both the sequence and age class groupings of long bone fusion of previous studies; 2. What is the sequence of tooth eruption and wear in these animals, are there differences between sheep and goat in these patterns, and how do these patterns relate to previous work; and, finally, 3. What is the correlation between long bone fusion patterns and tooth eruption and wear sequences in both sheep and goats and are there any systematic differences between these two key species, between different sexes of sheep and goats, or between animals from different collecting localities.

## The Sample

The sample of sheep and goat remains studied is curated by the Zoology Department of the Field Museum of Natural History in Chicago and was examined over five different research visits between 1996 and 2003. Many of these animals were collected from wild herds during several expeditions to Iran headed by then FMNH curator Douglas Lay (Lay 1967). Other specimens, including all the domestic specimens, were donated to the museum by Charles Reed, who collected these animals while a member of the Braidwood archaeological expeditions to north western Iraq and north eastern Iran (Fig. 1). A total of 39 goat specimens are included in this study, 37 of which are identified as wild bezoar goat (*Capra aegagrus,* species names follow the new rulings of the International Council for Zoological Nomenclature (2003)), and two of which represent unimproved domestic breeds of goats (*Capra hircus*) kept by local villagers. The goat sample includes 22 males and 17 females from six different collecting localities running from north to south along the spine of the Zagros, from the Caspian Sea to the Persian Gulf (Fig. 2).

The sheep sample consists of 61 animals, including 41 Asiatic mouflons (*Ovis orientalis*) and 15 urials (*Ovis vigni*) (Fig. 3), a more eastward member of the great arc of wild sheep (Clark 1964) collected around the shores of the Caspian Sea where they are known to readily hybridize with mouflons (Valdez *et al.* 1978). Five of the sheep specimens belong to a domestic fat tailed breed (*Ovis aries*) raised throughout the region by both nomadic and village herders. There are 30 females and 31 males in the sample. Six of the sheep collecting localities overlap with those for the goats. Four wild sheep specimens were collected in Baluchistan in far southeastern Iran (Fig. 1).

No estimate of age at death was made for any of the wild hunted specimens. Nor was there information recorded on the age at death of any of the domestic caprines included in the sample. There were no castrates in the sample. Pathologies were noted on four of the specimens.

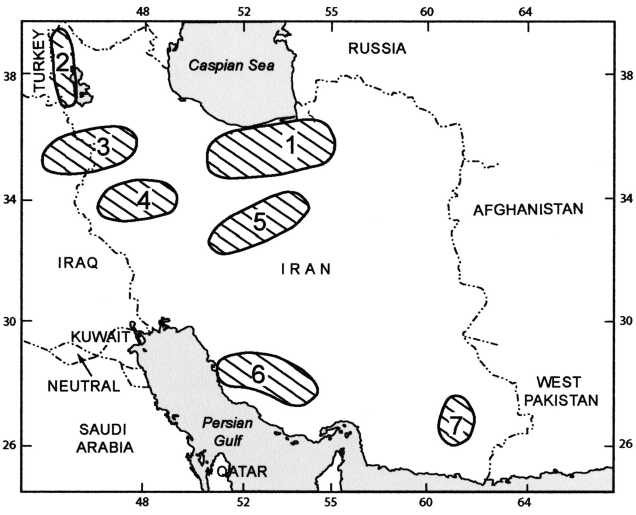


*Fig. 1. Collecting localities of sheep and goats used in this study.*

## Long Bone Fusion

### *Previous studies*

A number of previous studies have focused on trying to determine the sequence and timing of long bone fusion in sheep and goats (Figs 4 and 5; also see Moran and O'Connor 1994, 272–275 for a comprehensive summary of previous studies of epiphyseal fusion and tooth eruption and wear in sheep). Perhaps the best known and most widely used of these is included in the landmark article by Silver (1969). Silver based his work on a variety of sources, including 18th and 19th century records. No sample sizes or raw data are provided in this work that might allow for an assessment of the empirical robustness of this sequence. Other studies of epiphyseal fusion in domestic sheep include Garcia-Gonzalez's (1983) examination of Aragon sheep and Hatting's (1981) study of Gotland sheep. In a more recent study, Moran and O'Connor (1994) examined more than 150 animals, representing mixture of breeds from 'primitive' to modern crossbreeds housed in skeletal collections in Britain and Denmark. Males, females, and castrates were included in the sample. Data from castrates were excluded in compiling the fusion sequences and ages shown in Figs 4 and 5 since castration is know to have a profound impact on epiphyseal fusion in sheep and goats (Moran and O'Connor 1994; Davis 2000). Studies of goat epiphyseal fusion include Noddle's (1974) study of 54 domestic goats of mixed breeds and 20 feral goats culled from flocks in Britain, and Bullock and Rackham's (1982) study of 25 British feral goats.

While there is rough agreement in the sequence and, less so, in the timing of epiphyseal fusion reported in these various sources, there are also significant differences

| FMNH Number | Species | Sex | Region[1] | Fusion Group | Fusion Rank[2] | Dental Group | Dental Rank[2] |
|---|---|---|---|---|---|---|---|
| 97911 | *C. aegagrus* | F | 1 | B | 3 | IV | 5 |
| 97912 | *C. aegagrus* | F | 1 | B | 4 | IV | 4 |
| 58018 | *C. aegagrus* | M | 1 | G | 35 | XI | 35 |
| 97908 | *C. aegagrus* | M | 1 | E | 21 | V | 7 |
| 97910 | *C. aegagrus* | M | 1 | C | 9 | V | 10 |
| 97931 | *C. aegagrus* | M | 1 | G | 39 | nd | nd |
| 112505[3] | *C. aegagrus* | F | 2 | D | 18 | I | 1 |
| 99029 | *C. aegagrus* | F | 2 | G | 38 | X | 34 |
| 97913 | *C. aegagrus* | M | 2 | D | 14 | VI | 16 |
| 97914 | *C. aegagrus* | M | 2 | C | 7 | V | 8 |
| 44472 | *C. aegagrus* | F | 3 | E | 28 | VII | 19 |
| 84483 | *C. hircus* | F | 3 | D | 15 | V | 12 |
| 84486 | *C. aegagrus* | F | 3 | G | 34 | nd | nd |
| 35676 | *C. aegagrus* | M | 3 | G | 37 | X | 32 |
| 44466 | *C. aegagrus* | M | 3 | F | 33 | nd | nd |
| 57253 | *C. hircus* | M | 3 | D | 12 | V | 15 |
| 84485 | *C. aegagrus* | M | 3 | C | 8 | V | 14 |
| 92920 | *C. hircus* | F | 4 | E | 26 | IX | 30 |
| 92921 | *C. aegagrus* | F | 4 | E | 25 | VII | 22 |
| 92922 | *C. aegagrus* | F | 4 | D | 17 | V | 11 |
| 92923 | *C. aegagrus* | F | 4 | E | 29 | VII | 23 |
| 92924 | *C. aegagrus* | M | 4 | C | 6 | IV | 6 |
| 92925 | *C. aegagrus* | M | 4 | E | 22 | VIII | 29 |
| 97919 | *C. aegagrus* | F | 5 | E | 23 | VII | 18 |
| 97930 | *C. aegagrus* | F | 5 | D | 20 | VIII | 27 |
| 97916 | *C. aegagrus* | M | 5 | A | 2 | III | 2 |
| 97917 | *C. aegagrus* | M | 5 | D | 11 | V | 9 |
| 97920 | *C. aegagrus* | M | 5 | A | 1 | III | 3 |
| 97929 | *C. aegagrus* | M | 5 | D | 16 | VIII | 26 |
| 57949 | *C. aegagrus* | F | 6 | E | 27 | VII | 24 |
| 97921 | *C. aegagrus* | F | 6 | F | 31 | VII | 21 |
| 97925 | *C. aegagrus* | F | 6 | G | 36 | VII | 20 |
| 97926 | *C. aegagrus* | F | 6 | F | 30 | VIII | 28 |
| 57935 | *C. aegagrus* | M | 6 | D | 19 | VII | 25 |
| 57937 | *C. aegagrus* | M | 6 | D | 13 | VI | 17 |
| 57938 | *C. aegagrus* | M | 6 | C | 5 | V | 13 |
| 57943 | *C. aegagrus* | M | 6 | E | 24 | X | 33 |
| 97924 | *C. aegagrus* | M | 6 | F | 32 | IX | 31 |
| 97927 | *C. aegagrus* | M | 6 | D | 10 | nd | nd |

*Fig. 2. FMNH Goat Sample (*Capra *sp.). [1] = Collecting localities are shown in fig. 1, [2] = Age order from youngest to oldest, [3] = Mismatch between mandible and post-cranial.*

among them. All fusion schemes suggest that there are generally four general stages of epiphyseal fusion that roughly correspond to the first four years of life. However, the sequence, timing, and sometimes even the bones included in each of the four fusion groups vary. The earliest group of fusing bones in all schemes (Fusion Group A in Figs 4 and 5) is comprised of bones that fuse in the first year of life. In most sources, Group A includes the proximal radius, the glenoid process of the scapula, the acetabulum of the pelvis, and the distal humerus, but the sequence of fusion varies from study to study. Moreover, while all sources agree that these bone fuse sometime in the first year of life, both Hatting and Garcia-Gonzalez set the fusion of these bones within the first six months of life, while Silver places fusion of all of these elements in the second six months. In the fusion schemes of Moran and O'Connor and in Noddle, the proximal radius is the earliest fusing bone, fusing within the first six months of life, while the remaining elements in this group fuse in the second six months.

The second general fusion group (B) usually includes the first and second phalanx, although Noddle also includes the scapula and the distal humerus in this group. Most authors put the fusion age of these bones at between about 11 to 16 months. Once again, however, both Hatting and Garcia-Gonzalez cite earlier ages of fusion for these bones (between five to nine months), while Bullock and Rackham give the oldest ages of fusion at somewhere between 12 and 35 months of age.

Group C in most schemes contains the distal tibia and both distal metapodials, although there is variation in bones included in this group, as well as in the sequence and timing of their fusion. Most authors place the fusion of the distal tibia somewhat earlier than the distal metapodials. However, Silver maintains that the distal tibia and the distal metacarpal both fuse at about the

| FMNH Number | Species | Sex | Region[1] | Fusion Group | Fusion Rank[2] | Dental Group | Dental Rank[2] |
|---|---|---|---|---|---|---|---|
| 58015 | *O. vigne* | F | 1 | G | 55 | XI | 53 |
| 58019 | *O. vigne* | F | 1 | F | 43 | VI | 32 |
| 58020 | *O. vigne* | F | 1 | C | 9 | IV | 8 |
| 58024 | *O. vigne* | F | 1 | D | 18 | IV | 12 |
| 58063 | *O. vigne* | F | 1 | E | 28 | V | 14 |
| 58091 | *O. vigne* | F | 1 | E | 26 | V | 19 |
| 152003 | *O. vigne* | F | 1 | E | 23 | V | 21 |
| 58014 | *O. vigne* | M | 1 | D | 17 | V | 18 |
| 58021 | *O. vigne* | M | 1 | D | 12 | V | 15 |
| 58022 | *O. vigne* | M | 1 | C | 10 | IV | 11 |
| 58062 | *O. vigne* | M | 1 | G | 61 | IX | 46 |
| 58064 | *O. vigne* | M | 1 | G | 51 | X | 50 |
| 58089 | *O. vigne* | M | 1 | G | 52 | VII | 36 |
| 152002 | *O. vigne* | M | 1 | G | 49 | nd | nd |
| 152004 | *O. vigne* | M | 1 | G | 53 | nd | nd |
| 58039 | *O. orientalis* | F | 2 | D | 13 | IV | 6 |
| 58045 | *O. orientalis* | F | 2 | G | 60 | X | 51 |
| 58047 | *O. orientalis* | F | 2 | E | 29 | V | 20 |
| 58048 | *O. orientalis* | F | 2 | F | 34 | VII | 37 |
| 58057 | *O. orientalis* | F | 2 | B | 3 | II | 1 |
| 58058 | *O. orientalis* | F | 2 | F | 32 | V | 22 |
| 58065 | *O. orientalis* | F | 2 | F | 39 | V | 16 |
| 58069 | *O. orientalis* | F | 2 | B | 2 | II | 2 |
| 58070 | *O. orientalis* | F | 2 | G | 54 | VII | 40 |
| 58071 | *O. orientalis* | F | 2 | G | 44 | IX | 47 |
| 152006 | *O. orientalis* | F | 2 | F | 35 | nd | nd |
| 152008 | *O. orientalis* | F | 2 | D | 14 | nd | nd |
| 58035 | *O. orientalis* | M | 2 | F | 37 | VII | 42 |
| 58036 | *O. orientalis* | M | 2 | G | 50 | IX | 48 |
| 58037 | *O. orientalis* | M | 2 | E | 30 | VI | 33 |
| 58038 | *O. orientalis* | M | 2 | D | 15 | V | 17 |
| 58040 | *O. orientalis* | M | 2 | D | 20 | V | 13 |
| 58041 | *O. orientalis* | M | 2 | G | 58 | XII | 54 |
| 58042 | *O. orientalis* | M | 2 | G | 46 | VII | 39 |
| 58043 | *O. orientalis* | M | 2 | F | 36 | VII | 43 |
| 58044 | *O. orientalis* | M | 2 | D | 16 | VI | 26 |
| 58046 | *O. orientalis* | M | 2 | G | 57 | nd | nd |
| 58072 | *O. orientalis* | M | 2 | A | 1 | II | 3 |
| 152007 | *O. orientalis* | M | 2 | F | 40 | nd | nd |
| 58031 | *O. orientalis* | F | 3 | G | 56 | IX | 49 |
| 58033 | *O. orientalis* | F | 3 | F | 33 | V | 23 |
| 58034 | *O. orientalis* | F | 3 | G | 43 | VII | 38 |
| 152005 | *O. orientalis* | F | 3 | G | 47 | VIII | 44 |
| 57254 | *O. aries* | M | 3 | C | 6 | IV | 9 |
| 57255 | *O. aries* | M | 3 | E | 24 | VI | 28 |
| 58032 | *O. orientalis* | M | 3 | E | 25 | VI | 31 |
| 58094 | *O. aries* | M | 3 | C | 5 | IV | 7 |
| 84488 | *O. orientalis* | M | 3 | C | 8 | IV | 10 |
| 92927 | *O. aries* | F | 4 | D | 22 | nd | nd |
| 92928 | *O. aries* | F | 4 | G | 59 | X | 52 |
| 98161 | *O. orientalis* | M | 4 | F | 38 | VI | 34 |
| 98162 | *O. orientalis* | M | 4 | D | 19 | VI | 29 |
| 97957 | *O. orientalis* | F | 5 | G | 48 | VI | 35 |
| 97958 | *O. orientalis* | F | 5 | E | 31 | VI | 27 |
| 97959 | *O. orientalis* | F | 5 | C | 7 | III | 5 |
| 97960 | *O. orientalis* | M | 5 | D | 21 | VI | 25 |
| 97973 | *O. orientalis* | M | 6 | G | 45 | VIII | 45 |
| 97985 | *O. orientalis* | F | 7 | E | 27 | VI | 30 |
| 97986 | *O. orientalis* | F | 7 | B | 4 | III | 4 |
| 97983 | *O. orientalis* | M | 7 | F | 41 | VII | 41 |
| 97984 | *O. orientalis* | M | 7 | D | 11 | VI | 24 |

*Fig. 3. FMNH Sheep Sample (*Ovis *sp.). [1] = Collecting localities are shown in fig. 1, [2] = Age order from youngest to oldest.*

| Silver (1969) Sheep | | | | Hatting (1981) Gotland Sheep | | | | Garcia-Gonzalez (1983) Aragon Sheep | | | | Moran and O'Connor (1994) Various European Sheep Breeds | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group | Bone[1] | Order[2] | Age[3] | Group | Bone | Order | Age | Group | Bone | Order | Age | Group | Bone | Order | Age |
| A | Scap | 1 | 6–8 | A | P.Rad | 1 | 2–4 | A | P.Rad | 1 | 1.5–3 | A | P.Rad | 1 | 4.5–6 |
| A | Pelvis | 2 | 6–10 | A | D.Hum | 1 | 2–4 | A | D.Hum | 2 | 2–4 | A | Scap | 2 | 6–9 |
| A | P.Rad | 3 | 10 | B | 1 Phl | 2 | 6–9 | A | Scap | 3 | 3–4 | A | D.Hum | 3 | 6–10.5 |
| A | D.Hum | 3 | 10 | C | D. Tib | 3 | 13–15 | B | 2 Phl | 4 | 5–7 | B | 2 Phl | 4 | 11–12 |
| B | 1 Phl | 4 | 13–16 | C | Calc | 4 | 15–17 | B | 1 Phl | 5 | 6–8 | B | 1 Phl | 4 | 11–12 |
| B | 2 Phl | 4 | 13–16 | C | D.Mc | 5 | 15–22 | C | D.Tib | 6 | 12–15 | C | D.Tib | 5 | 13–23 |
| C | D. Tib | 5 | 18–24 | C | D.Mt | 6 | 15–23 | C | D.Mc | 7 | 12–18 | C | Calc | 6 | 13–30 |
| C | D. Mc | 5 | 18–24 | C | P.Fem | 6 | 15–23 | C | D.Mt | 7 | 12–18 | C | D.Mc | 7 | 15–24 |
| C | D. Mt | 6 | 20–28 | C | D.Fem | 6 | 15–23 | C | Calc | 7 | 12–18 | C | P.Ulna | 8 | 15–30 |
| D | Calc | 7 | 30–36 | D | D.Rad | 7 | 15–30 | D | P.Ulna | 8 | 18–30 | C | D.Mt | 8 | 15–30 |
| D | P. Ulna | 8 | 36 | D | P.Tib | 7 | 15–30 | D | P.Fmr | 9 | 18–36 | D | P.Fmr | 9 | 23–36 |
| D | P. Fmr | 8 | 36 | D | P.Hum | 8 | 24–30 | D | D.Rad | 9 | 18–36 | D | D.Rad | 10 | 23–40 |
| D | D.Rad | 8 | 36 | – | Scap | nd | nd | D | P.Tib | 10 | 24–36 | D | D.Fmr | 11 | 24–40 |
| D | P.Tib | 9 | 36–42 | – | Pelvis | nd | nd | D | D.Fmr | 10 | 24–36 | D | P.Hum | 12 | 36–42 |
| D | D.Fmr | 9 | 36–42 | – | 2 Phl | nd | nd | D | P.Hum | 11 | 30–42 | D | P.Tib | 13 | 36–45 |
| D | P.Hum | 9 | 36–42 | – | P.Ulna | nd | nd | – | Pelvis | nd | nd | – | Pelvis | nd | nd |

*Fig. 4. Fusion sequences and ages of fusion from previous studies on sheep. [1] = Abbreviations for elements, Scap – scapula, P.Rad – proximal radius, D.Hum – distal humerus, 1 Phl – first phalanx, 2Phl – second phalanx, D.Tib – distal tibia, D.Mc – distal metacarpal, D.Mt – distal metatarsal, P.Ulna – proximal ulna, Calc – calcaneus, P.Fmr – proximal femur, D.Rad – distal radius, P.Tib – proximal tibia, D.Fmr – distal femur, P.Hum – proximal humerus; [2] = Order of fusion from earliest to latest, [3] = Age in months.*

| Noddle (1974) British Breeds and Feral Goats | | | | Bullock and Rackham (1982) British Breeds and Feral Goats | | | |
|---|---|---|---|---|---|---|---|
| Group | Bone | Order | Age | Group | Bone | Order | Age |
| A | P.Rad | 1 | 4–9 | A | P.Rad | 1 | < 12 |
| B | Scap | 2 | 9–11 | A | D.Hum | 1 | < 12 |
| B | 2 Phl | 3 | 9–12 | A | Scap | 2 | ~ 12 |
| B | 1 Phl | 4 | 11–12 | A | Pelvis | 2 | ~ 12 |
| B | D.Hum | 5 | 11–13 | B | 1 Phl | 3 | > 12 < 35 |
| C | D.Tib | 6 | 19–24 | B | 2 Phl | 3 | > 12 < 35 |
| C | D.Mc | 7 | 23–24 | C | D.Tib | 4 | ~ 36 |
| C | D.Mt | 7 | 23–24 | C | D.Mc | 5 | ~ 48 |
| D | P.Fmr | 8 | 23–36 | C | D.Mt | 5 | ~ 48 |
| D | P.Tib | 8 | 23–36 | C | P.Fmr | 5 | ~ 48 |
| D | Calc | 9 | 23–48 | C | D.Fmr | 5 | ~ 48 |
| D | D.Fmr | 9 | 23–48 | D | Calc | 6 | > 48 < 60 |
| D | P.Hum | 9 | 23–48 | D | D.Rad | 7 | > 47 < 71 |
| D | D.Rad | 10 | 33–48 | D | P.Tib | 7 | > 47 < 71 |
| – | Pelvis | nd | nd | D | P.Hum | 8 | > 47 < 83 |
| – | P. Ulna | nd | nd | D | P.Ulna | 9 | ~ 71 |

*Fig. 5. Fusion sequences and ages of fusion from previous studies on goats. (Abbreviations concur with fig. 4).*

same time, slightly earlier than the metatarsal. Both studies by Hatting and Moran and O'Connor place the fusion of the tuber calis of the calcaneus between the fusion of the distal tibia and the distal metacarpal. Moran and O'Connor also include the proximal ulna in this group, while others place it with later fusing bones. Hatting and Bullock and Rackham include the proximal and distal femur in this group, fusing at about the same time as the distal metapodials.

While all sources put the fusion of Group C bones at greater than 12 months of age, there is considerable variation in the start and end ages given for the fusion of these bones. Once again, Garcia-Gonzalez reports some of the youngest ages, maintaining that all bones in this group fuse between 12 to 18 months of age. Hatting also reports an early start date for the fusion of bones in this group, with fusion beginning between 13 to 15 months for the distal tibia and calcaneus and completed by 23 months for the distal metapodials and the proximal and distal femur. Moran and O'Connor also put the start date for fusion of these bones at about 13 to 15 months, but give a later completion date of between 24 to 30 months. Silver and Noddle place the fusion of the bones in this stage at between about 18 to 28 months. Once again Bullock and Rackham report the oldest ages of fusion for the bones in this group, maintaining that distal tibia

fuses at about 36 months, and the metapodials and the proximal and distal femur at about 48 months.

The latest fusion group, Group D, is also the largest and most variable. Bones included in the latest fusion stage are generally the calcaneus, the proximal and distal femur, the distal radius, the proximal tibia, and the proximal humerus. In some sources this group might be further sub-divided into slightly earlier and slightly later fusing elements, although there is little agreement over the bones included in these sub-groups or their age at fusion. There is also a considerable amount of overlap in start and end dates of fusion among these later fusing bones. In Silver's scheme, the proximal ulna, calcaneus, proximal femur, and distal radius fuse between about 30 to 36 months of age, while the proximal tibia, distal femur, and proximal humerus are the latest fusing bones, at about 36 to 42 months. In Hatting, the distal radius and proximal tibia fuse between 15 to 30 months, while the latest fusing bone is the proximal humerus, which fuses between 24 and 30 months. Garcia-Gonzalez's scheme places the fusion of the proximal ulna, the proximal femur, and the distal radius between 18 to 36 months, while the start point for fusion of the proximal tibia and the distal femur is put at 24 months and the end date at 36 months. As in Hatting, Garcia-Gonzalez's scheme has the proximal humerus as the latest fusing bone, with fusion set at 30 to 42 months. In Moran and O'Connor, the earlier fusing bones in this final stage are the proximal femur, the distal radius, and the distal femur, which fuse between about 23 to 42 months. The latest fusing bones in this fusion scheme are the proximal humerus and proximal tibia, which are reported to fuse between 36 to 45 months.

Among Noddle's goats (Fig. 5) the earlier fusing bones in this final stage are the proximal femur and the proximal tibia, both of which are said to fuse between 23 to 36 months. The calcaneus, distal femur, and the proximal humerus are next with fusion ages set between 23 to 48 months and the latest fusing bones is the distal radius, which is reported to fuse between 33 and 48 months. Bones included in this final fusion stage in Bullock and Rackham's scheme are the calcaneus, distal radius, proximal tibia, and proximal humerus, all of which are said to fuse sometime after about 47 months of age. Fusion of the proximal ulna is said to occur at about 71 months, while the proximal humerus fuses sometime between 48 to 83 months.

Given the mix of different samples on which these different fusion schemes are based, it is difficult to pinpoint the source of variability in the sequence and timing of epiphyseal fusion among them. There are several factors that might be at work here. Genotypic differences between different taxa (sheep and goats) and breeds of animals might be expected to affect both the sequence and, to a large degree, the timing of bone fusion. Phenotypic factors are also likely to have some impact on epiphyseal fusion. In particular, variation in nutrition, either resulting from differences in pasture and fodder quality or variations in the age at weaning (or both), are especially likely to have an effect on the rate or timing of bone fusion. In addition, while castrates were excluded from the data presented here, differences in the sex of animals included in the various samples may have played some role in the ages of fusion (Moran and O'Connor 1994, 273). It is also possible that pure stochastic variation between these samples, which are of widely varying size and composition, may play some role here.

A more superficial examination of these data might suggest that taxon plays the major role in the timing, if not the sequence, of bone fusion, with goats tending to have more delayed epiphyseal fusion than sheep. However, it is important to note that a number of the goats in both Noddle's sample and all the goats studied by Bullock and Rackham were feral animals that probably had a much lower plane of nutrition than the improved breeds of Gotland and Aragon sheep used in the Hatting and the Garcia-Gonzalez samples. Nutritional deficiencies, especially those early in life, are known to result in delays in epiphyseal fusion (Palsson and Verges 1952, cited in Moran and O'Connor 1994, 274). In this light, the somewhat older ages of fusion given for the sheep on which the Silver and the Moran and O'Connor schemes are based may stem from the inclusion of 'semi-wild' and 'primitive' breeds of animals in both these samples that might be expected to have a somewhat lower plane of nutrition.

### *The FMNH caprines*

For a number of reasons, the sheep and goats included in the Field Museum of Natural History's collections provide a more directly comparable modern analog for the ancient populations of caprines that are of interest to archaeologists. First, even the 'primitive' breeds and feral animals included in other studies of this nature represent the end-point of millennia of selective breeding by humans. This is not a problem with the FMNH sample, which is largely comprised of wild animals. Second, while progressive degradation of the natural habitat of these wild caprines has undoubtedly had some nutritional impact, the feeding regimes of these animals are still more likely to be closer to those of ancient wild and early domestic animals from this region. Even the handful of domestic animals in the sample were derived from unimproved breeds, raised by local villagers or by migrating nomadic tribesmen, that occupied the same general region and roughly the same kinds of pasture as the wild animals in the sample. In contrast, modern European breeds are likely to receive improved fodder or other nutritional supplements, or be subject to accelerated weaning schedules, that can have a profound impact on rates of bone fusion (Moran and O'Connor 1994, 274) Third, comparisons between sheep and goat are also easier

to make with this sample given the general overlap in the collecting localities for these animals. Finally, the almost even representation of males and females in both the sheep and goat samples allows for control of any sex-linked bias. There are no castrates in either the wild or the domestic specimens eliminating any concern over resultant delays in fusion in castrated animals. The major limitation of the sample is the lack of independent information on the age of death of the different animals.

Fusion data for the FMNH goats and sheep are presented by specimens in Fig. 6 (for goats) and Fig. 7 (for sheep) in the Appendix. Four different possible fusion states were identified. Bones were scored as unfused (*U*) if the epiphysis was clearly separate from the diaphysis, even if remaining tendons and tissue held the two together. They were scored as early fusion (***J***) if there were signs of fusion but the junction between the epiphysis and the diaphysis was still partly open. Bones were scored as in late fusion (**L**) if the epiphysis and diaphysis were tightly joined, but there was still a faint line of fusion evident, and as fused (**F**) if the epiphysis and diaphysis were tightly joined and the line of fusion no longer apparent. Specimens were ranked and ordered from youngest to oldest on the basis of the number of unfused elements and the status of the fusing and fused bones. General fusion stages were then determined for both the goat and the sheep samples based on an assessment of the patterning seen in the individual specimens (Figs 6–14 in Appendix).

Although there is some variability, especially in later fusing bones, the same seven general fusion groups were evident in both sheep and goats. Group A (Fig. 8) is reserved for specimens in which the proximal radius is in early fusion. The acetabulum of the pelvis was also in early fusion in one of the goat specimens placed in Group A and the distal humerus was in early fusion in the sheep specimen. However, these bones were also undergoing early fusion in other specimens of sheep and goats in which the proximal radius was in late fusion, indicating that the proximal radius fuses at a slightly earlier point than these other bones and merits being placed in its own fusion group.

In Group B (Fig. 9), the proximal radius is in late fusion while the pelvis, the glenoid process of the scapula, and distal humerus are generally in early fusion. All other elements are unfused. In Group C (Fig. 10) the second and first phalanges come into play, while earlier fusing bones are mostly in either late fusion or fully fused. All other bones are unfused, save for three goat specimens where the radius and ulna were identified as fusing together, although it is sometime difficult to assess the state of fusion of these bones in less cleaned specimens. The phalanges were grouped together into a single fusion stage because they seem to fuse at a distinctly different time than all other bones. When these two bones are fusing, all other earlier fusing bones are either in late fusion or fused, and all later fusing bones are unfused. However for both the goats and sheep, it is clear that the second phalanx fuses before the first phalanx.

Group D (Fig. 11) centers on the fusion of the distal tibia, distal metacarpal, and the distal metatarsal. Once again, while the fusion of these three bones seems to happen in a distinct period of time between both earlier and later fusing bones, they do not all fuse at the same time. In both sheep and goats the distal tibia fuses slightly earlier than the metapodials, which fuse at about the same time. In some of the goats the radius and the ulna were also beginning to fuse together at this point, though in other specimens these bones fused at the same time as bones included in age class C, and in still others, the fusion of the ulna to the radius happened at the same time as the fusion of other later fusing bones. The radius and the ulna were never fused in any of the sheep examined, regardless of age. Given the longer period of time over which these bones fuse together in goats, and the fact that they never seem to fuse in sheep, the fusion of the radius and ulna is not included in the fusion scheme presented here. It is important to note, however, that in most goats the radius and the ulna only really begin to fuse at about Stage D or E. Therefore, using the lack of fusion of a radius to an ulna as a means of distinguishing sheep from goat bones is not acceptable. A radius or ulna that is found unfused to its companion bone might as easily be a goat killed before it reached these later fusion stages as a sheep.

Fusion patterns are a little less clear cut in Group E (Fig. 12), which includes the tuber calis of the calcaneus, the proximal and distal femur, the proximal ulna, the distal radius, and the distal tibia. As was done for earlier fusion groups, these bones were grouped together because they come into fusion after all other earlier fusing bones are either fully fused or in late fusion. Among the goats there is little apparent consistency in the sequence in which these bones fuse, although there is some suggestion that the calcaneus tends to fuse a bit earlier than the other bones included in Group E. Among the sheep the calcaneus is clearly the first in this group to fuse, followed by the proximal femur (both the caput and the trochanter), distal femur, and the proximal ulna, with the distal radius and the proximal tibia the last to fuse among this group of bones. It is not clear if the difference between sheep and goats in the sequence of fusion of bones included in this fusion stage is an artifact of the FMNH sample (i.e. there is a great range of ages in the sheep that fall into this general stage, while the goats in the sample are all closer in age), or a real difference in the sequence of epiphyseal fusion of sheep and goats. Regardless, what is clear is that in both sheep and goats the fusion of these bones occurs at a distinct phase of an animal's life.

Group F (Fig. 13) is reserved for specimens whose proximal humerus is entering early fusion. The fusion of the proximal humerus is separated from the other later fusing bones because its fusion seems be somewhat delayed. In both sheep and goat there are a number of

specimens in which all the bones included in the earlier age class E are either in early or late fusion, while the proximal humerus remains unfused. Once the proximal humerus enters early fusion, the bones included in Group E are generally either in early or late fusion, and all other earlier fusing bones are fully fused.

The final fusion stage, Group G (Fig. 14), is reached when the proximal humerus is in either late fusion or fully fused. Once the proximal humerus reaches this advanced phase of fusion, the bones included in Fusion Group E are also either in late fusion or fully fused, while all other earlier fusing elements are fully fused.

Fig. 15 presents the revised fusion sequence for sheep and goats based on the FMNH collections. This fusion scheme varies from earlier ones primarily in the details of the order of bone fusion and the number of fusion groups defined. While earlier fusion schemes all seemed to recognize four general fusion groups, there are seven groups evident in the FMNH data. The extra groups are gained by splitting the earliest fusion group in other schemes into two separate groups (A and B), with Group A based on the fusion of the proximal radius and Group B based on the fusion of the scapula, pelvis, and distal humerus. The large group of late fusing bones that constitute Group D in most sources is divided into three groups with the addition of two final age classes based on the fusion of the proximal humerus (F and G).

The sequence of fusion of these different elements is remarkably consistent across this large sample of animals with no apparent variation between male and female caprines or between animals from different collecting localities. The few domestic specimens in the sample also show no variation in sequence of epiphyseal fusion from the wild ones. Moreover, with the exception of the large group of bones in Group E, the sequence of bone fusion is remarkably consistent in both sheep and goats. And even this later fusion group includes the same suite of bones. The only possible difference here is that in sheep the distal radius and the proximal tibia seem to enter early fusion slightly earlier than the proximal and distal femur and the proximal ulna. In goats these bones seem to fuse as a group in no particular order. But again this may be more an artifact of the sample used than real difference in the sequence of late fusing bones in sheep and goats.

Without independent information on the age of the FMNH caprines, the age ranges of the different fusion stages identified here cannot be determined with any certainty. Using earlier studies based on domestic sheep and goats is problematic for reasons discussed above. However, if one extrapolates from these earlier studies based on known age specimens, a rough hypothetical aging scheme can be offered and used as grounds for comparison to ages derived from the analysis of tooth eruption and wear of the same specimens. The ages offered in Fig. 15 for the various fusion stages identified in the FMNH collection draw principally from Silver, Moran and O'Connor, and Noddle. Hatting and Garcia-Gonzalez's aging schemes are given less weight since both seem quite young compared to other sources, perhaps because both are based exclusively on single breeds of sheep that may have a higher plane of nutrition than the mixed and feral animals included in other studies. By the same token, Bullock and Rackham's aging scheme is also given less weight in drawing the age estimates presented in Fig. 15. Age estimates provided by Bullock and Rackham are quite broad, probably a result of the spotty coverage of different age classes in their sample. In particular, the very late ages given for the later fusing bones are almost certainly an artifact of the sample on which the study was based. Given the lack of an unimpeachable empirical tether for these age estimates, and the range of ages given in the sources used, the ages assigned here are based on the half year increments which best correspond to the ages given in other sources. No attempt is made to assign ages for the final two fusion stages based on the degree of fusion for the proximal humerus. Group F is simply listed as older than the 48 month end point set for epiphyseal fusion of the bones in Stage E. Group G is similarly said to be older than Group F, with no attempt to fix a specific age range for point in which the proximal humerus enters late fusion or is at last fully fused.

## Tooth Eruption and Wear

### *Previous studies*

Dental aging systems for sheep and goats are based on a combination of genotypic and phenotypic factors that drive the eruption and wear of teeth. As with epiphyseal fusion, the sequence and timing of tooth eruption in sheep and goats are hard wired within the genetic code for each species, although variations in nutrition likely play some role in the timing of tooth eruption. By the same token, although there are likely genetically controlled factors that determine the pattern and rate of tooth attrition (i.e. tooth morphology and bio-mechanics of mastication), the primary factors determining tooth attrition are the types of pasturage and fodder consumed and, especially, the ingestion of soil along with pasturage (Moran and O'Connor 1994, 270). Constructing a reliable dental system for determining age at death, then, requires combining tooth eruption sequences that might be expected to be more universally found across closely related taxa, with attritional patterns more likely to vary among even closely related taxa raised under different conditions. Despite this somewhat awkward marriage of convenience, there is a surprising degree of agreement between dental aging systems that combine dental eruption and wear. Ages for the eruption of cheek teeth of sheep and goats cited in most studies of known age populations of sheep and goat are in remarkably close agreement (Fig. 16). As

was the case for epiphyseal fusion, differences in the timing of tooth eruption are most likely linked to differences in nutrition, with feral, 'rough', or 'semi-wild' animals with delayed eruption rates when compared to carefully tended 'improved' breeds. Even so, the overall agreement on the sequence and timing of tooth eruption is quite good. Even North American wild dall sheep (*Ovis dalli*) and the much more distantly related mountain goat (*Oreamnos americanus*) have eruption schedules that closely mirror domestic breeds of sheep and goat. An almost identical eruption schedule is documented in Himalyan Thar (*Hemitragus jemlahicus*) a species of wild goat introduced to the Southern Alps of New Zealand (Caughley 1965).

There are two commonly used systems for noting tooth wear in sheep and goats, that developed by Grant and the system devised by Payne. Grant's (1982) method is essentially a "floating" system that determines relative stages of wear of individual teeth, but does not provide the estimated ages at which these various stages are reached. In contrast, Payne's system (Payne 1973, Deniz and Payne 1982) looks at eruption and wear patterns across the mandible and is linked directly to age classes derived from studies of modern sheep from a village herd in central Turkey and, most significantly, on observations of tooth wear in living animals from an experimental herds of Angora goats under the care of the Turkish Ministry of Agriculture.

Subsequent applications of Payne's system to known age populations have resulted in some refinement of the methods for noting wear patterns (Payne 1987, Zeder 1985 and 1991), adjustment and sharpening of age stages (Jones, this volume), and cautionary notes about the reliability of older age classes (Moran and O'Connor 1994). Overall though, the Payne system has proven quite robust and reliable. In particular, Jones' remarkable work with living British sheep published here goes a long way toward demonstrating the validity of both the sequence of tooth wear patterns identified in this earlier work and the ages at which these stages of wear are generally reached. Fig. 17 presents the age classes defined in Payne's system using the notational system developed by Zeder (1985 and 1991). The correlation between Zeder's notational system and that published by Payne in 1987, as well as its correlation with Grant's system, is provided in Fig. 18.

Unlike Payne's notational system that assigns a different sequence of letters and numbers to the wear patterns for each tooth, Zeder's system assigns the same sequence of numbers to all teeth when they reach equivalent stages of wear. For example, in Zeder's system stage '09' is reserved for teeth when they just begin to show signs of wear, '17' is assigned to teeth worn to the point when either one or two enamel islands (depending on the number of cusps the tooth has) are isolated by dentine from the outer enamel covering of the tooth, and '25' is reserved for teeth where all internal enamel is worn away and the occlussal surface contains nothing but dentine. In contrast, under Payne's system Zeder's stage '17' would be stage '9A' for the M1 and M2, or 11G for the M3, 14L for the dp4, or 9A, 9S, or 9T for the P4. Although perhaps less familiar, Zeder's system is followed here partly as a matter of convenience since it was the system used in the study of dental wear of the FMNH collections. This system also makes it easier to follow wear patterns across the jaw.

Payne system identifies nine different groups labeled A–I. In Zeder's notational system, the letters used to designate Payne's dental groups are replaced with roman numerals (I–IX). Again while Payne's dental groups may be more familiar, the Zeder system is used here to avoid confusion when contrasting longbone fusion groups with dental groups. In contrast to aging systems based epiphyseal fusion which only cover the first four to five years of life, dental age schema cover a much wider span – up to 10 or more years, which is essentially the entire life span of an animal. The first five dental groups (I–V following Zeder) are defined primarily on the basis of eruption and early wear stages deciduous and permanent teeth. Each of these early dental groups represents an increasingly longer span of time, ranging from 0–2 months for Group I to 2–3 years for Group V. Groups VI–IX are based solely on attrition of permanent premolars and molars. Once again, the age ranges represented by these groups also expand in duration in the later stages. Group V represents 2–3 year old animals, Group VIII represents 6–8 year olds, and the final group, Group IX represents animals in the range of 8–10+ years.

### *The FMNH caprines*

Dental aging was applied to all sheep and goat specimens in the FMNH collection from Iran and Iraq that had both post-cranial and cranial bones. For the goats, this was 35 specimens (Figs 2 and 19), and 54 specimens for the sheep (Figs 3 and 20). Stages of cheek tooth eruption and wear were recorded for the right and left sides of the mandible using Zeder's notations. The system was also adapted for maxillary teeth, but these data are not reported here. As was done for the post-cranial epiphyseal fusion patterns, individual specimens of sheep and goats were ranked and ordered from youngest to oldest based on eruption and wear patterns, and then grouped into general dental age classes (Figs 19, 20 and 21–30).

Figs 21–30 present the FMNH dental data in a way that makes it easier to visualize eruption and wear patterns across the mandible for each dental group in both goats (on the left) and sheep (on the right). The deciduous and permanent cheek teeth are arrayed along the horizontal axis of the table, while the various wear stages are displayed on the vertical axis (Fig. 15, see Zeder 1991, 92 for the definition of these stages). Stages 02 through 08 represent eruption stages before the tooth begins to experience wear. Stage 09, highlighted in bold double

lines, represents the beginning of tooth wear on the mesial cusps. Stages 10 through 12 are early wear stages where enamel is just beginning to wear and dentine is first exposed on various cusps, while stages 13 through 17 represent more active wear stages in which progressive amounts of dentine exposed as individual cusps are joined together. Stage 17, in which central enamel islands are separated from the enamel covering the outside of the teeth by a sea of dentine (equivalent to Payne's long lived stage 9a for the P4, M1, and M2 and his 11G for the M3), is also highlighted by double bolded lines. Stages 18 through 26 represent late wear stages in which the remnants of enamel on the occlusal surfaces of the teeth are eroded away until they disappear altogether (stage 25) and the tooth is worn to the root (stage 26). The number of specimens with teeth in different wear stages is noted, with .5 representing a specimen in which teeth on the right and left of the jaw are in different states of wear. Shading covers the range of wear stages observed for the teeth of the individuals included in each age class. As with epiphyseal fusion patterns, dental eruption and wear patterns for sheep and goats are quite similar to one another. However, there are systematic differences between sheep and goats in all dental groups that suggest differences in mastication in these two species. Group I (Fig. 21) is present in only one very young goat in which the deciduous premolars are just entering early wear stages and the M1 is visible in the crypt but below the surface of the bone. Group II (Fig. 21), found in only three sheep specimens, is typified by deciduous premolars in more active wear, the M1 in later stages of eruption but either unworn or just beginning to wear, and the M2 visible in the crypt but not yet beginning to erupt.

There are both goat and sheep specimens represented in Group III (Fig. 22), which allows an initial look at differences in tooth wear patterns in these two species. Group III is defined by deciduous premolars in late wear stages (after stage 17), the M1 in active wear but before stage 17, and the M2 either just visible in the crypt or beginning to erupt, but still below the surface of the bone. Sheep vary from goats in that the dP2 is also entering late wear stages, while in the goats only the dP3 and dP4 are in these more advanced stages of wear and the dP2 is essentially unworn.

The deciduous premolars are in late or final stages of wear in Group IV (Fig. 23), although in some specimens the permanent premolars can be seen pushing up through the bone under the deciduous premolars. The M1 is in active wear reaching the keystone wear stage 17, the M2 is either erupting but not yet level with the other cheek teeth, or just entering early wear, and the M3 is usually still either only visible in the crypt or just beginning to erupt but still below the top of the surface of the mandible. In two goat specimens the M3 is further along in the eruption process, but still yet to come into wear. Once again the deciduous premolars of the sheep in this age class show more even wear across all teeth, with the dP2 worn in a similar fashion as the dP3 and dP4. In contrast in the goat the dP3 seems to take the brunt of attritional force, while both the dP4 and especially the dP2 are less worn.

Mandibles placed in Group V (Fig. 24) have permanent premolars entering more active wear stages. The M1 remains at stage 17, while the M2 is undergoing active wear but generally has yet to reach this plateau stage. The M3 is either still erupting or just entering early wear stages. In both sheep and goats the M1 seems to be experiencing the greatest degree of wear at this stage. However, as seen in earlier dental groups wear seems to be more evenly spread across the cheek teeth in sheep, while in goats the wear is more narrowly focused.

The majority of cheek teeth reach stage 17 during the subsequent Group VI (Fig. 25), when the P3, P4, M1, and M2 all reach this wear stage. The M3 is entering more active wear stages, with the M3 in sheep more likely to experience more wear than in goats.

The P3, P4, and, to a lesser extent, the M1 all breach this plateau stage of wear and enter later wear stages in Group VII (Fig. 26). The M2 remains at stage 17 and the M3 is still undergoing active wear leading up to stage 17. In sheep the M3 is more likely to reach stage 17, and the M1 is more likely to breach this stage. In goats wear seems more narrowly focused on the P3 and P4.

During Dental Group VIII (Fig. 27) the P3 through M1 reach stage 20 wear in which only a single isolated enamel island remains on the tooth. The M2 remains at stage 17 and the M3 is either at or close to stage 17. In the sheep the P2 might also reach the more advanced wear stage 20. In Group IX mandibles (Fig. 28) the M1 is in final stages of wear and may reach stage 25 in which all internal enamel is eroded from the tooth. The M2 and M3 may be either at stage 17 or beginning to breach this stage and enter the later wear stages. The premolars generally remain at stage 20, although in goats the P2 remains essentially unworn.

The P3 and P4 loose all traces of central enamel (stage 25) in the Group X mandibles (Fig. 29) and the M1 may be worn to the root (stage 26). Although the M2 may remain at stage 17, most are in the final stages of erosion of the central enamel islands. The M3 remains at stage 17. Once again the P2 in sheep is clearly undergoing more wear than in goats.

The final two dental groups (Fig. 30) are distinguished from one another by the wear of the M3. In Group XI all teeth but the M3 are worn to the root, while the M3 is in late wear. The M3s in Group XII mandibles are either devoid of any central enamel or worn to the root.

The dental groups represented in the FMNH caprines are directly analogous to the original Payne system (Figs 31 and 32). The only departure from this system is that two of the original dental groups can now be divided into two younger and older phases of wear. Zeder's old Group IV (Group D in Payne's system) can be divided into earlier and later dental groups (new groups IV and V).

Zeder's original Group VII (Payne's Group G) now becomes new dental groups VIII and IX. Figs 31 and 32 also gives age estimates for these various age classes by retaining the ages assigned to these wear classes by Payne (and subsequently empirically supported by other studies). In the case of the two new dental groups, the age range assigned to the original group is divided evenly. Original Group IV (Payne's D) which covered 12 to 24 months is now divided into Group IV (12–18 months) and Group V (18–24 months), and original Group VII (Payne's G) which covered 4 to 6 years, is divided into groups VIII (4–5 years) and IX (5–6 years).

It is important to remember that the assignment of ages to these dental groups needs to be treated as hypothetical since the true age of the FMNH caprines is not known. While these data strongly suggest that mandibluar teeth in both sheep and goats follow regular patterns of eruption and wear, it is entirely possible that the mandibles of different animals will arrive at these different states of eruption and wear at different ages. This is especially true for the later dental groups that are based solely on attritional patterns, (see also Moran and O'Connor 1994, 282).

A particularly interesting result of this examination has been the detection of systematic differences in the patterns of wear in sheep and goat mandibular teeth. While both sheep and goat follow the same general sequence of mandibular tooth wear, there is a consistent tendency for wear to be more evenly spread across the cheek tooth row in sheep. In contrast mandibular tooth wear in goats seems more narrowly focused on one or two teeth, with the primary load of attritional force shifting among different teeth (primarily the P3, P4, and M1) as the mandible undergoes progressive wear. Possible reasons for this difference and its effect on the rates of tooth wear in sheep and goats are discussed below. There is no detectable difference in the sequence of tooth eruption and wear in the few domestic sheep and goats in the sample.

## Reconciling Fusion and Dental Groups

One of the outstanding questions in the construction of mortality profiles from archaeological remains centers on how well profiles based on epiphyseal fusion data correspond to those based on dental eruption and wear. Direct comparability between mortality profiles constructed with these different measures of age requires that the estimation of age at death of an individual using epiphyseal fusion be the same as the age estimate based on the individual's state of dental eruption and wear. And yet the correlation between these two different measures has never been adequately tested. While we are hampered by the lack of definitive information on the age at death of the FMNH caprines, we can look at the degree of correspondence between fusion and dental age estimates in a couple of ways.

### *Comparability within taxa*

One measure of the degree of correlation between these two different ways of estimating age is to compare the rank age orders for the FMNH sheep and goats based on fusion and dental data. Matching fusion and dental rank orders of sheep and goats provided in Figs 2 and 3 clearly demonstrates a very close correspondence between these two measures of age. Whether using parametric or non-parametric tests, the correlation between the fusion and dental age orders of both the sheep and goats are highly correlated at better than the .00005 level of probability. Pearson product-moment correlations for fusion and dental rank order for goats is 0.917 and for goats 0.832. Using Spearman's Rho statistics the correlation between fusion and dental rank order is .831 for goats and .916 for sheep.

But how well do the actual age estimates for the FMNH sheep and goats based on fusion data correspond to those based on tooth eruption and wear? Fig. 33 presents a matrix for goats and sheep that looks at the corespondence between fusion and dental groups. Fusion groups are arranged across the horizontal axis along with estimated age ranges for each group derived from published sources. Dental groups are arrayed along the vertical axis, and are also shown with estimated ages. Cells in the matrix that represent a total overlap between the fusion and dental age estimates are shaded in dark grey, while those that represent overlap with either the start or the end of the age range estimates are shaded in light grey. The number of specimens that fall into each cell is indicated, with goats on the left and sheep on the right.

The correspondence between age estimates for the fusion and the dental groups is generally fairly good. There is total overlap in the age estimates based on fusion and dental data (specimens that fall in the dark grey cells) in 55% of the goat specimens and 57% of the sheep. An additional 33% of the goats and 25% of the sheep specimens fall in the overlap zones for either the beginning or the end of the age ranges given by fusion and dental data (specimens in light grey cells). This means that there is general agreement between these two estimators in 82% of the FMNH sheep and 88% of the goats. To a certain extent, the better degree of overlap between dental and fusion age estimates in goats may be attributable to the fact that dental age ranges are primarily based on Deniz and Payne's study of a known age population of Angora goats.

The agreement between the fusion based age estimates and the dental estimates is closest in the younger groups (A–C fusion groups and I–V dental groups). Older groups show more variability, perhaps because older dental groups are based solely on attritional patterns that are likely to show more variation in the ages at which these different wear states are reached. Without an independent measure of the age of FMNH caprines it is impossible to assess the correspondence between the dental age assignment and fusion age assignment of individuals placed in

the final two open-ended fusion groups (F and G). However, it is promising that in both sheep and goats (with only one exception for each), individuals in Fusion Group F (48+ months) generally fall into younger dental groups than individuals placed in the final Fusion Group G (48++ months).

### *Comparability between taxa*

There is evidence of consistent systematic differences between sheep and goats in the way in which the fusion and dental groups correspond to one another. Age estimates for sheep based on dental data are uniformly younger than those provided by fusion data, while the dental ages for goats are consistently older than age estimates based on fusion data. For example, both of the goats classified in Fusion Group A fall into Dental Group III, but the sheep specimen assigned to Fusion Group A has a dental pattern that places it in Dental Group II. The goat specimens in Fusion Group B both fall into Dental Group IV. In contrast, two of the sheep in Fusion Group B fall into Dental Group II and one falls into Dental Group III. This pattern becomes even more exaggerated in subsequent Fusion Groups C, D, and E.

Moreover, goats in older fusion groups (i.e. D and E) tend to fall into a much wider range of dental groups than do sheep. Goats with fusion patterns that place them in Fusion Group D (18–30 months), for example, have dental patterns that place them in Dental Groups V, VI, and VIII (covering a range of ages from 18 months to 5 years). In contrast, sheep placed in Fusion Group D fall into either Dental Group IV, V, or VI (from 12–36 months). Goats placed in Fusion Group E (30–48 months) may fall into Dental Groups VII-X (from 4–10 years), while sheep classified as belonging to Fusion Group E have dental patterns that place them in Dental Groups V and VI (18–36 months).

Both of these patterns suggest that there are systematic differences between sheep and goat in either the timing of epiphyseal fusion or in the rate of tooth eruption and wear. Specifically, the FMNH data indicates that either sheep teeth erupt and wear at a slower rate than goat teeth (and conversely that goat teeth erupt and wear faster than sheep teeth), or that the long bones of sheep fuse earlier than in goats (and conversely that goat long bones fuse later than in sheep). Again the lack of independent data on age at death of the FMNH caprines means that this question cannot be definitively resolved. But there are indications from the review of previous literature and from data provided by this study of the FMNH caprines that may help distinguish between these two options.

It is difficult to attribute these patterns to differences in fusion schedules of sheep and goat long bones. Previous studies of fusion rates in known age animals suggest generally close correspondence between sheep and goats in the ages at which bones fuse. And while Noddle's (1974) and Bullock and Rackham's (1982) studies suggest some delay in epiphyseal fusion in goats compared to sheep, these differences are more likely attributable to differences in nutritional intake between feral goats and closely tended improved breeds of sheep. The nearly identical sequence of bone fusion in the FMNH goats and sheep is also suggestive of close correspondence in the timing of fusion. In fact, the only potential differences in epiphyseal fusion sequence detected in the FMNH sheep and goats occur in the late fusion stages represented by the bones included in Fusion Group E. Yet the mismatch in the fusion and dental groups between sheep and goats is evident across all groups, not just in this late stage of development.

As with epiphyseal fusion, most studies indicate that schedules of tooth eruption in sheep and goats are quite similar (see Fig. 16). This means that if the source of the disparity lies in the dental age estimates, it is most likely attributable to differences in rates of tooth wear – specifically that sheep teeth wear more slowly than goat teeth. Yet on the surface this conclusion would seem somewhat counterintuitive. Sheep are much more committed grazers, while goats utilize a much higher proportion of browse in their diets (Redding 1981, 47–49). As a result, sheep teeth are subjected to a higher degree of attritional agents, both in the form of the silica bodies derived from pasture grasses that typically have a very high silica content (Delores Piperno, personal communication 2003), and from the higher proportion of soil that is likely to be ingested along with graze. Goats also move more quickly between feeding localities than sheep, while sheep are more likely to stay in one spot cropping all grasses and forbs as close to the ground as possible and thereby taking in more soil as they graze (Redding 1981, 48). The amount of soil ingested with graze is known to be a primary agent in differential tooth wear in caprines (Moran and O'Connor 1994, 270). There may also be differences in the amount of rumination needed to break down higher silica content pasturage, which would also subject sheep teeth to more wear. Therefore, one might think that sheep teeth should wear faster than goats, not slower as suggested here.

However, there is some reason to believe that the greater potential for tooth attrition in the feeding ecology of sheep selected for both structural and behavioral features that serve to slow the rate of tooth wear in these animals. First, sheep teeth in general are said to show greater hypsodonty than goats (Payne 1985, 143), an adaptation aimed at prolonging the use life of teeth that make it seem as if sheep teeth wear more slowly. There is simply more tooth that must be worn down to progress between various wear stages. Second, patterns of mandibular tooth wear observed in the FMNH caprines suggest differences in the mechanics of mastication in sheep and goat that may also be an adaptation of different feeding ecologies. Whether deciduous or permanent teeth, tooth wear in sheep was more even across all cheek teeth, from the P2 (or dP2) to the M3. In goats, primary wear

was more narrowly focused on central cheek teeth, with attritional load shifting across these teeth as the mandible undergo progressive wear. Distributing the load more evenly across the tooth row would likely lessen the attrition of individual teeth and therefore slow the rate of tooth wear in sheep.

These differences in feeding ecology, degree of hypsodonty, and chewing mechanics may also contribute to the tendency for goats to show a wider range of dental groups associated with older fusion groups. Redding (1981, 49) reports that goats will vary their diets depending on the nature and the quality of pasturage available, mixing variable amounts of graze and browse plants depending on local conditions. While they prefer to graze on grasses and forbs if available, they will also browse on a wide array of other plants and plant parts if adequate graze is not available. As a result, goats in regions with better quality pasturage may have a higher intake of graze, exposing their teeth to more silica and soil ingested while grazing which both cause teeth to wear more quickly. Goats in regions with poorer pasture may consume a higher proportion of browse with less potential for tooth attrition. The amount of graze and browse that any one goat consumes over its lifetime will also likely vary seasonally or perhaps over years with variable amounts of rainfall. The effect of the variable intake of attrition causing agents in goats might be exacerbated by their masticatory mechanics, which tend to focus load more narrowly across the tooth row. Moreover, if indeed goat teeth show less hypsodonty than sheep teeth, they will also be more likely to reflect variable rates of wear more dramatically than sheep. Sheep, on the other hand are more obligate grazers and will live off of stored body fat when adequate graze is not available (Redding 1981, 49). Thus the more consistent, tighter correlation between fusion and dental groups in sheep may be the result of their more exclusive commitment to grazing on a narrower range of plants, their higher crowned teeth, and the more even spread of load across the cheek teeth in sheep. There are no detectable differences in wear patterns between wild and domestic sheep and goats.

### *Comparability between sexes*

Figs 34 and 35 look at the correlation between fusion and dental age estimates for male and female specimens with goats in Fig. 34 and sheep in Fig. 35. In both sheep and goats, male specimens consistently fall into older dental groups than females. This pattern is especially clear in the larger sample of sheep examined. For example, there are eight male sheep with fusion patterns that place them in Fusion Group D (18–30 months). Four of these animals have dental patterns that place them in Dental Group V (18–24 months) and four fall into Dental Group VI (24–36 months). In contrast, the two female sheep in Fusion Group D have dental patterns that place them in Dental Group IV (12–18 months). In goats, six males in Fusion Group D range in dental age between Dental Group V to Dental Group VIII (18 months to 5 years), while two female goats in Fusion Group D fall into Dental Group V (18–24 months).

Once again, the most likely source of this difference lies in rates of dental attrition rather than in the timing of epiphyseal fusion. While there is some indication of delayed fusion in the long bones of male sheep, the data are somewhat contradictory. Hatting reports earlier fusion in females for eight of fourteen epiphyses examined and earlier fusion in males for the remaining six epiphyses (Hatting 1981, cited in Moran and O'Connor 1994, 273). These results are similar to those of Moran and O'Connor (1994, 280) who found slightly earlier fusion in females in bones that fuse before about 24 to 30 months of age, while males show slightly earlier fusion in bones that fuse at about 36 months or later. The difference in fusion age between males and females noted by Moran and O'Connor, however, is never more than seven months and usually less than three.

In contrast, Deniz and Payne (1982, 187) found clear differences in rates of tooth wear in male and female Angora goats. While rates of wear in males and females were about the same in animals in their first year, there was a tendency toward more rapid wear in males at about two years that seemed to increase with age. Deniz and Payne attribute this difference to the larger body size of males that becomes more marked after one year and to higher levels of activity in males which probably requires more intake to sustain.

### *Comparability between collecting localities*

It is also possible that differences in pasture quality will affect rates of epiphyseal fusion and tooth eruption schedules in sheep and goats. Differences in pasture plants and in local soil conditions (i.e. the hardness and amount of grit inclusions in soil), in particular, are often mentioned as a potential factor in the rate of tooth wear attrition in these animals. Therefore, it is not unreasonable to expect some differences in the rates of epiphyseal fusion and tooth eruption and wear in FMNH sheep and goats from different collecting localities.

Regrettably, it is difficult to directly test this possibility with the FMNH caprines, since the sample animals from any one collecting locality is quite small (Figs 2 and 3). However judging from this limited sample, there do not appear to be any marked differences between animals from different collecting localities. In all localities, the dental age estimates for the sheep are consistently younger than the fusion age estimates and the dental age estimates for the goats for are consistently older than fusion age estimates. The patterning observed for males and females also holds true across all localities. Both larger samples and better information on local pasture conditions are needed before this question can be adequately addressed.

## Conclusions

At its outset this paper raised a number of questions about the sequence and timing of epiphyseal fusion and tooth eruption and wear and the correlation between these measures of age. The study of the FMNH caprines has shed a significant amount of light on these questions. First, it has established a clear sequence of bone fusion that is consistently found in both sheep and goats. Regardless of the ages at which these various bones fuse, the order of fusion from youngest (proximal radius) to oldest (proximal humerus) is firmly established here (see Figs 8–15). This new sequence based on this large population of wild animals will hopefully resolve open questions about the precise sequence of epiphyseal fusion in early hunted and herded sheep and goats. Whether put together in fusion groups (A–G) or singly as individual bones, this should be the sequence used when ordering elements in an archaeological assemblage in the process of constructing mortality profiles for sheep, goats, or sheep and goats as a combined sample.

Similarly, this study establishes a progressive pattern of tooth eruption and wear in caprines. Even with the clear differences noted between sheep and goats, the general phases of eruption and wear identified here are consistently seen in both. Once again, regardless of age assignment, these stages can be used to provide a rank order of specimens (see Figs 21–32). One of the innovations of this study is that it looks at wear patterns across the mandible rather than in individual teeth. Most other studies of dental eruption and wear, even those that make age assignments based on eruption and wear states of a number of different cheek teeth, tend to look at eruption and, especially, wear patterns of individual teeth in isolation (i.e. Deniz and Payne 1982, Moran and O'Connor 1994, Jones this volume). While much valuable effort has been devoted to refining and attempting to calibrate individual stages of tooth wear of individual teeth, to some extent some of this very tight focus may lose sight of important mandible wide patterns with direct relevance to the reconstruction of reliable dental mortality profiles. Specifically what one misses in this approach is an understanding of the overall mechanics of wear across a mandible over the course of an animal's life. Looking at wear across the mandible has made it possible to detect subtle but, I believe, important patterns of wear that represent new dental groups that provide greater resolution to sequence of dental eruption and wear in these animals. Most importantly, this study highlighted hitherto unnoticed differences in the wear patterns of sheep and goat teeth that may have a significant impact on the use of dental patterns in the construction of mortality profiles in sheep and goats.

As to the correlation between fusion and dental aging techniques, clearly there is a high degree of correlation between the ranked age order of specimens using these two methods. Moreover, there is reasonable consistency in the placement of both sheep and goats in the various fusion and dental groups. With some exceptions in older animals, the majority of goats whose fusion patterns place them in certain fusion groups are consistently placed in the same dental groups. The same is true for sheep, although the correspondence between groups varies. Even in the later fusion groups with defined end points (D and E) where there is more variability in corresponding dental group assignments, the majority of specimens fall into one or two adjacent groups.

The problem comes in reconciling which fusion groups correspond to which dental groups. There are clear systematic differences in the correspondence between fusion and dental groups in sheep and goats that have been attributed primarily to differential rates of tooth wear related to differences in feeding ecology, tooth morphology, and chewing mechanics in sheep and goats. There are also differences in the correspondence between these age estimators in males and females which have similarly been linked primarily to differential rates of wear. These species and sex-linked differences in rates of tooth wear raise serious questions about the application of dental based age estimates to samples which contain both sheep and goats, as well as a mixture of males and females. If, for example, one accepts that all sheep and goats classified in Fusion Group D actually fall within the same closely defined age range (18–30 months), these animals have a range of dental patterns that place them in dental groups spanning an estimated age range of four years (from 1–5 years). Sheep and goat specimens classified in Fusion Group E (estimated to range from 30–48 months) fall into 6 different dental groups that are estimated to range from 18 months to 8 years.

Until recently the only criteria for distinguishing between the teeth of sheep and goat were those presented by Payne (1985) developed for certain milk teeth and unworn M1s, useful only in classification of young individuals. A recent article by Halstead and Collins (2002) presents criteria for adult teeth, both premolars and molars, as well as for the mandible. However, in both studies there are few unambiguous criteria that can be used to reliably distinguish between the teeth and mandible of goats and sheep. Most of the criteria presented in these papers will only distinguish specimens that are clearly goats from specimens that are either sheep or goat. Thus, we are still lacking definitive criteria that allow secure separation of sheep and goat mandibles and mandibular teeth that can then be used to devise species-specific dentally based mortality profiles. There are no methods I know of for distinguishing males from females on the basis of tooth or mandibular morphology.

In contrast, there are a number of solid criteria for distinguishing between the long bones of sheep and goat that make it possible to compute species-specific fusion based age profiles with some confidence (Zeder and Lapham, in preparation). Moreover, in goats (and to a certain extent in sheep) marked sex-linked dimorphism

in the size of skeletal elements can be used to reliably separate male from female animals (at least in wild assemblages and those dating to the earlier phases of the domestication process). Thus, with large assemblages it is possible to construct mortality profiles that are both species and sex-specific (see Zeder 2001). If fusion sequences and timing are indeed reasonably consistent across taxa and sexes as concluded here, then even fusion-based mortality profiles based on mixed samples of sheep and goats, males and females may be more likely to reflect the actual age order sequence of the mixed population than a dental profile based on a mixed sample.

This is not to say that dental-based mortality profiles are not useful. Indeed they are, especially in looking at ages that fall outside the upper limit of fusion data. However, profiles based on these data need to be considered as rough approximates of mortality, especially in the later ages when variations in rates of attrition have the greatest impact. Attempts to affix precisely defined age estimates to these older groups are out of line with the fact that different animals will reach these different stages of dental wear at somewhat different ages.

As to the calibration of the fusion and the dental groups defined here, for the moment the age ranges drawn from previous studies of known age populations will have to suffice. A planned study of annual increments in the horn sheaths of the FMNH sheep and goats will provide another estimate of the ages of these animals that may help with the calibration of the fusion and dental groups defined in this study. It may also help to test some of the conclusions drawn here about the reliability of fusion and dental criteria and the mortality profiles based on them. But for now these age estimates should be taken as rough proxies of age and age order that can be used for comparison between samples, rather than a firm empirically grounded estimates of the actual age at death.

*Acknowledgements*

Field Museum of Natural History staff Lawrence Heaney, William Stanley, Michi Schulenburg, and Deborah Bekken facilitated access to the large skeletal collections of modern caprines. In addition to the author, the research teams on the various visits to the FMNH included Amy Aisen, Susan Arter, Naomi Cleghorn, Lesley Gregoricka, Margaret Heirs, Heather Lapham, Justin Lev-Tov, Sarah McClure, Scott Rufolo, and Bruce Smith. Bruno Frolich offered useful advice on the statistical analysis. Many thanks are owed Deborah Ruscillo for her patience and fortitude in the production of this volume and in the organization of the fine symposium on which it is based.

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# Appendix

| Fusion Group | FMNH # | P. Rad[1] | Pelvis | Scap | D. Hum | 2 Phl | 1 Phl | D. Tib | D. Mc | D. Mt | Rad & Ulna | Calc | P. Fmr (ball) | P. Fmr (troch)[2] | D. Fmr | P. Ulna | D. Rad | P. Tib | P. Hum |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 97920 | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| A | 97916 | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| B | 97911 | **L** | *U* | ***J*** | ***J*** | – | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| B | 97912 | **L** | ***J*** | ***J*** | ***J*** | – | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 57938 | **F** | **L** | ***J*** | **L** | – | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 92924 | **F** | **F** | **L** | **F** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 97914 | **F** | **F** | **F** | **F** | **F** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 84485 | **F** | **F** | **F** | **F** | **L** | ***J*** | *U* | *U* | *U* | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 97910 | **F** | **F** | **F** | **L** | – | **L** | *U* | *U* | – | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97927 | **F** | **F** | **F** | **F** | **F** | **F** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97917 | **F** | **F** | **F** | **F** | **F** | ***J*** | *U* | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 57253 | **F** | **F** | **F** | **F** | **F** | **L** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 57937 | **F** | **F** | **F** | **F** | – | **F** | **L** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97913 | **F** | **F** | **F** | **F** | **F** | **F** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 84483 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | *U* | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97929 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | ***J*** | **L** | ***J*** | *U* | *U* | ***J*** | *U* | *U* | *U* | *U* | *U* |
| D | 92922 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 112505 | **F** | **F** | **F** | **F** | – | **F** | **L** | **L** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 57935 | **F** | **F** | **F** | **F** | – | **F** | **F** | **L** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97930 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **L** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97908 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| E | 92925 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | **F** | ***J*** | **L** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* |
| E | 97919 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **F** | ***J*** | *U* | ***J*** | ***J*** | ***J*** | ***J*** | ***J*** | ***J*** | *U* |
| E | 57943 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | **L** | **F** | ***J*** | ***J*** | ***J*** | ***J*** | ***J*** | *U* | *U* |
| E | 92921 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | ***J*** | ***J*** | ***J*** | ***J*** | ***J*** | ***J*** | *U* |
| E | 92920 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | ***J*** | ***J*** | ***J*** | ***J*** | **L** | ***J*** | *U* |
| E | 57949 | **F** | **F** | **F** | **F** | - | **F** | **F** | **F** | **F** | **L** | **L** | **L** | **L** | **L** | **L** | ***J*** | *J* | *U* |
| E | 44472 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | ***J*** | **L** | **L** | **L** | **L** | ***J*** | ***J*** | ***J*** | *U* |
| E | 92923 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **L** | **L** | **L** | *U* | **L** | ***J*** | *U* |
| F | 97926 | **F** | **F** | **F** | **F** | **F** | F | **F** | **F** | **F** | ***J*** | **L** | ***J*** | **L** | ***J*** | ***J*** | ***J*** | ***J*** | ***J*** |
| F | 97921 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **L** | **L** | ***J*** | ***J*** | ***J*** |
| F | 97924 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | ***J*** | **L** | **L** | **L** | **L** | **L** | ***J*** |
| F | 44466 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **L** | **L** | **L** | **L** | ***J*** |
| G | 84486 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | ***J*** | **L** | **L** | **L** | **L** | **L** | **L** |
| G | 58018 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | **L** | **F** | **F** | **L** | **L** | **L** | **L** |
| G | 97925 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | **L** | **L** | **F** | **F** | **L** | **L** | **L** |
| G | 35676 | **F** | – | **F** | **F** | – | – | **L** | **F** | **F** | **F** | **F** | **L** | **F** | **F** | **F** | **F** | **F** | **L** |
| G | 99029 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | **F** | **F** | **F** | **F** | **F** |
| G | 97931 | **F** | **F** | **F** | **F** | – | – | **F** | **F** | **F** | **F** | **F** | **L** | **F** | **F** | **F** | **F** | **F** | **F** |

*Fig. 6. Epiphyseal fusion in FMNH goats in rank order from youngest to oldest (U – unfused, **J** – early fusion, **L** – late fusion, **F** – fully fused, see text for explanation). [1] – see fig. 4 for element abbreviations, [2] – Troch – trochanter.*

| Age Class | FMNH # | P. Rad[1] | Pelvis | Scap | D. Hum | 2 Phl | 1 Phl | D. Tib | D. Mc | D. Mt | Rad & Ulna | Calc | P. Fmr (ball) | P. Fmr (troch)[2] | D. Fmr | P. Ulna | D. Rad | P. Tib | P. Hum |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 58072 | ***J*** | *U* | *U* | ***J*** | – | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| B | 58069 | **L** | *U* | *U* | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| B | 58057 | **L** | ***J*** | ***J*** | ***J*** | – | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| B | 97986 | **L** | ***J*** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 58094 | **F** | ***J*** | **L** | **L** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | – | *U* | *U* | *U* |
| C | 57254 | **F** | **L** | **L** | **L** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 97959 | **L** | ***J*** | **L** | **L** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 84488 | **F** | **F** | **F** | **F** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 58020 | **F** | **F** | **F** | **F** | – | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| C | 58022 | **F** | **F** | **F** | **F** | **F** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97984 | **F** | **F** | **F** | **F** | **L** | **L** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 58021 | **F** | **F** | **F** | **F** | – | **F** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 58039 | **L** | **F** | **F** | **F** | **F** | **L** | **L** | *U* | *U* | *U* | *U* | – | – | *U* | *U* | *U* | *U* | *U* |
| D | 152008 | **F** | **F** | **F** | **F** | – | **L** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 58038 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 58044 | **F** | **F** | **F** | **F** | – | **F** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 58014 | **F** | **F** | **F** | **F** | – | **F** | **F** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 58024 | **F** | **F** | **F** | **F** | – | **F** | **L** | ***J*** | ***J*** | *U* | *U* | – | – | *U* | *U* | *U* | *U* | *U* |
| D | 98162 | **F** | **F** | **F** | **F** | **F** | **L** | **L** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 58040 | **F** | **F** | **F** | **F** | – | **F** | **L** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 97960 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| D | 92927 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | **F** | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| E | 152003 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| E | 57255 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **L** | *U* | **L** | *U* | *U* | *U* | *U* | *U* | *U* | *U* |
| E | 58032 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | *U* | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* | *U* |
| E | 58091 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | ***J*** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* |
| E | 97985 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | *U* | **L** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* |
| E | 58063 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **F** | **F** | *U* | ***J*** | ***J*** | ***J*** | *U* | *U* | *U* | *U* | *U* |
| E | 58047 | **F** | **F** | **F** | **F** | – | **F** | **L** | **L** | **L** | *U* | ***J*** | **L** | ***J*** | ***J*** | **L** | *U* | *U* | *U* |
| E | 58037 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **L** | ***J*** | ***J*** | ***J*** | **L** | ***J*** | ***J*** | *U* |
| E | 97958 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **L** | **L** | **L** | ***J*** | **L** | ***J*** | ***J*** | *U* |
| F | 58058 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **L** | **L** | **L** | ***J*** | ***J*** | ***J*** | ***J*** | ***J*** |
| F | 58033 | **F** | **F** | **F** | – | – | **F** | **F** | **F** | **F** | *U* | **L** | ***J*** | **L** | ***J*** | **L** | ***J*** | ***J*** | ***J*** |
| F | 58048 | **F** | **F** | **F** | **F** | – | **L** | **F** | **L** | **L** | *U* | **L** | ***J*** | **L** | ***J*** | **L** | **L** | ***J*** | ***J*** |
| F | 152006 | **F** | **F** | **F** | **F** | **F** | **F** | **L** | **L** | **L** | *U* | **L** | **L** | ***J*** | ***J*** | **L** | **L** | ***J*** | ***J*** |
| F | 58043 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **L** | ***J*** | **L** | **L** | ***J*** | ***J*** |
| F | 58035 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **L** | ***J*** | **L** | **F** | ***J*** | ***J*** |
| F | 98161 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | ***J*** | **L** | **L** | **L** | ***J*** |
| F | 58065 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **L** | **L** | **L** | ***J*** | ***J*** |
| F | 152007 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | ***J*** | **F** | ***J*** | **F** | **F** | **F** | **F** | **F** | ***J*** |
| F | 97983 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **L** | **F** | **L** | **L** | ***J*** |
| F | 58019 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **L** | **L** | **F** | **L** | ***J*** |
| G | 58034 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | ***J*** | **F** | **L** | **F** | **F** | **F** | **L** |
| G | 58071 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **L** | **L** | **L** | ***J*** | **L** |
| G | 97973 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | ***J*** | **L** | **L** | **F** | **F** | **L** | **L** |
| G | 58042 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **L** | **L** | **L** | **L** | **L** | **L** |
| G | 152005 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | ***J*** | **F** | **L** | **F** | **L** | **L** | **L** | **L** | **L** |
| G | 97957 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **L** | **F** | **L** | **L** | **L** |
| G | 152002 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **F** | **F** | **L** | **L** | **L** |
| G | 58036 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **F** | **L** | **L** | **F** | **L** |
| G | 58064 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | ***J*** | **F** | **L** | **F** | **L** | **F** | **F** | **L** | **L** |
| G | 58089 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **L** | **L** | **L** | **L** | **L** | **L** | **L** | **L** |
| G | 152004 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | ***J*** | **F** | **L** | **F** | **L** | **F** | **F** | **F** | **L** |
| G | 58070 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **F** | **F** | **F** | **L** | **L** |
| G | 58015 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | ***J*** | **F** | **L** | **F** | **F** | **F** | **F** | **F** | **L** |
| G | 58031 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **F** | **F** | **F** | **F** | **L** |
| G | 58046 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **F** | **F** | **F** | **F** | **L** |
| G | 58041 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **L** |
| G | 92928 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | ***J*** | **F** | **L** | **F** | **L** | **F** | **L** | **L** | **F** |
| G | 58045 | **F** | **F** | **F** | **F** | – | **F** | **F** | **F** | **F** | *U* | **F** | **L** | **F** | **F** | **F** | **F** | **F** | **F** |
| G | 58062 | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** | *U* | **F** | **F** | **F** | **F** | **F** | **F** | **F** | **F** |

*Fig. 7. Epiphyseal fusion in FMNH sheep in rank order from youngest to oldest (U – unfused,* ***J*** *– early fusion,* ***L*** *– late fusion,* ***F*** *– fully fused, see text for explanation). [1] – see fig. 4 for element abbreviations, [2] – Troch – trochanter.*

| | Goats n=2 | | | | | Sheep n=1 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Unfused | Early Fusing | Late Fusing | Fully Fused | | Unfused | Early Fusing | Late Fusing | Fully Fused |
| P.Rad | | 2 | | | P.Rad | | 1 | | |
| Pelvis | 1 | 1 | | | Pelvis | 1 | | | |
| Scap | 2 | | | | Scap | 1 | | | |
| D.Hum | 2 | | | | D.Hum | | 1 | | |
| 2Phl | 2 | | | | 2Phl | | | | |
| 1Phl | 2 | | | | 1Phl | 1 | | | |
| D.Tib | 2 | | | | D.Tib | 1 | | | |
| D.Mc | 2 | | | | D.Mc | 1 | | | |
| D.Mt | 2 | | | | D.Mt | 1 | | | |
| Rad/Ulna | 2 | | | | Rad/Ulna | 1 | | | |
| Calc | 2 | | | | Calc | 1 | | | |
| P.Fmr(b) | 2 | | | | P.Fmr(b) | 1 | | | |
| P.Fmr(t) | 2 | | | | P.Fmr(t) | 1 | | | |
| D.Fmr | 2 | | | | D.Fmr | 1 | | | |
| P.Ulna | 2 | | | | P.Ulna | 1 | | | |
| D. Rad | 2 | | | | D. Rad | 1 | | | |
| P. Tib | 2 | | | | P. Tib | 1 | | | |
| P. Hum | 2 | | | | P. Hum | 1 | | | |

*Fig. 8. Fusion groups for goats and sheep – Group A.*

| | Goats n=2 | | | | | Sheep n=3 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Unfused | Early Fusing | Late Fusing | Fully Fused | | Unfused | Early Fusing | Late Fusing | Fully Fused |
| P.Rad | | | 2 | | P.Rad | | | 3 | |
| Pelvis | 1 | 1 | | | Pelvis | 1 | 2 | | |
| Scap | | 2 | | | Scap | 1 | 2 | | |
| D.Hum | | 2 | | | D.Hum | | 3 | | |
| 2Phl | | | | | 2Phl | 2 | | | |
| 1Phl | 2 | | | | 1Phl | 3 | | | |
| D.Tib | 2 | | | | D.Tib | 3 | | | |
| D.Mc | 2 | | | | D.Mc | 3 | | | |
| D.Mt | 2 | | | | D.Mt | 3 | | | |
| Rad/Ulna | 2 | | | | Rad/Ulna | 3 | | | |
| Calc | 2 | | | | Calc | 3 | | | |
| P.Fmr(b) | 2 | | | | P.Fmr(b) | 3 | | | |
| P.Fmr(t) | 2 | | | | P.Fmr(t) | 3 | | | |
| D.Fmr | 2 | | | | D.Fmr | 3 | | | |
| P.Ulna | 2 | | | | P.Ulna | 3 | | | |
| D. Rad | 2 | | | | D. Rad | 3 | | | |
| P. Tib | 2 | | | | P. Tib | 3 | | | |
| P. Hum | 2 | | | | P. Hum | 3 | | | |

*Fig. 9. Fusion groups for goats and sheep – Group B.*

| | Goats n=5 | | | | | Sheep n=6 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Unfused | Early Fusing | Late Fusing | Fully Fused | | Unfused | Early Fusing | Late Fusing | Fully Fused |
| P.Rad | | | | 5 | P.Rad | | | 1 | 5 |
| Pelvis | | | 1 | 4 | Pelvis | | 2 | 1 | 3 |
| Scap | | 1 | 1 | 3 | Scap | | | 3 | 3 |
| D.Hum | | | 2 | 3 | D.Hum | | | 3 | 3 |
| 2Phl | | 1 | 1 | 1 | 2Phl | | 4 | | 1 |
| 1Phl | 2 | 1 | 1 | | 1Phl | 4 | | | 1 |
| D.Tib | 5 | | | | D.Tib | 6 | | | |
| D.Mc | 5 | | | | D.Mc | 6 | | | |
| D.Mt | 5 | | | | D.Mt | 6 | | | |
| Rad/Ulna | 3 | 2 | | | Rad/Ulna | 6 | | | |
| Calc | 5 | | | | Calc | 6 | | | |
| P.Fmr(b) | 5 | | | | P.Fmr(b) | 6 | | | |
| P.Fmr(t) | 5 | | | | P.Fmr(t) | 6 | | | |
| D.Fmr | 5 | | | | D.Fmr | 6 | | | |
| P.Ulna | 5 | | | | P.Ulna | 5 | | | |
| D. Rad | 5 | | | | D. Rad | 6 | | | |
| P. Tib | 5 | | | | P. Tib | 6 | | | |
| P. Hum | 5 | | | | P. Hum | 6 | | | |

*Fig. 10. Fusion groups for goats and sheep – Group C.*

| | Goats n=12 | | | | | Sheep n=12 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Unfused | Early Fusing | Late Fusing | Fully Fused | | Unfused | Early Fusing | Late Fusing | Fully Fused |
| P.Rad | | | | 12 | P.Rad | | | | 11 |
| Pelvis | | | | 12 | Pelvis | | | | 12 |
| Scap | | | | 12 | Scap | | | | 12 |
| D.Hum | | | | 12 | D.Hum | | | | 12 |
| 2Phl | | | | 12 | 2Phl | | | 1 | 5 |
| 1Phl | | 1 | 1 | 10 | 1Phl | | | 4 | 8 |
| D.Tib | 2 | 2 | 5 | 3 | D.Tib | | 2 | 8 | 2 |
| D.Mc | 4 | 3 | 4 | 1 | D.Mc | 7 | 3 | 1 | 1 |
| D.Mt | 5 | 1 | 5 | 1 | D.Mt | 7 | 3 | 1 | 1 |
| Rad/Ulna | 9 | 3 | | | Rad/Ulna | 12 | | | |
| Calc | 12 | | | | Calc | 12 | | | |
| P.Fmr(b) | 12 | | | | P.Fmr(b) | 10 | | | |
| P.Fmr(t) | 11 | 1 | | | P.Fmr(t) | 10 | | | |
| D.Fmr | 12 | | | | D.Fmr | 12 | | | |
| P.Ulna | 12 | | | | P.Ulna | 12 | | | |
| D. Rad | 12 | | | | D. Rad | 12 | | | |
| P. Tib | 12 | | | | P. Tib | 12 | | | |
| P. Hum | 12 | | | | P. Hum | 12 | | | |

*Fig. 11. Fusion groups for goats and sheep – Group D.*

| | Goats n=8 | | | | | Sheep n=9 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Unfused | Early Fusing | Late Fusing | Fully Fused | | Unfused | Early Fusing | Late Fusing | Fully Fused |
| P.Rad | | | | 8 | P.Rad | | | | 9 |
| Pelvis | | | | 8 | Pelvis | | | | 9 |
| Scap | | | | 8 | Scap | | | | 9 |
| D.Hum | | | | 8 | D.Hum | | | | 9 |
| 2Phl | | | | 7 | 2Phl | | | | 5 |
| 1Phl | | | | 8 | 1Phl | | | | 9 |
| D.Tib | | | 2 | 6 | D.Tib | | | 3 | 6 |
| D.Mc | | | 1 | 7 | D.Mc | | | 4 | 5 |
| D.Mt | | | | 8 | D.Mt | | | 4 | 5 |
| Rad/Ulna | 0 | 3 | 5 | | Rad/Ulna | 9 | | | |
| Calc | 1 | | 4 | 3 | Calc | | 5 | 4 | |
| P.Fmr(b) | 0 | 5 | 3 | | P.Fmr(b) | 2 | 5 | 2 | |
| P.Fmr(t) | 0 | 5 | 3 | | P.Fmr(t) | 3 | 5 | 1 | |
| D.Fmr | 1 | 4 | 3 | | D.Fmr | 6 | 3 | | |
| P.Ulna | 2 | 5 | 1 | | P.Ulna | 6 | 0 | 3 | |
| D. Rad | 1 | 5 | 2 | | D. Rad | 7 | 2 | | |
| P. Tib | 2 | 6 | | | P. Tib | 7 | 2 | | |
| P. Hum | 8 | | | | P. Hum | 9 | | | |

*Fig. 12. Fusion groups for goats and sheep – Group E.*

| | Goats n=4 | | | | | Sheep n=11 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Unfused | Early Fusing | Late Fusing | Fully Fused | | Unfused | Early Fusing | Late Fusing | Fully Fused |
| P.Rad | | | | 4 | P.Rad | | | | 11 |
| Pelvis | | | | 4 | Pelvis | | | | 11 |
| Scap | | | | 4 | Scap | | | | 11 |
| D.Hum | | | | 4 | D.Hum | | | | 10 |
| 2Phl | | | | 4 | 2Phl | | | | 4 |
| 1Phl | | | | 4 | 1Phl | | | 1 | 10 |
| D.Tib | | | | 4 | D.Tib | | | 1 | 10 |
| D.Mc | | | | 4 | D.Mc | | | 2 | 9 |
| D.Mt | | | | 4 | D.Mt | | | 2 | 9 |
| Rad/Ulna | | | 1 | 3 | Rad/Ulna | 10 | 1 | | |
| Calc | | | 1 | 3 | Calc | | | 4 | 7 |
| P.Fmr(b) | | 2 | 2 | | P.Fmr(b) | | 3 | 8 | |
| P.Fmr(t) | | | 4 | | P.Fmr(t) | | 1 | 5 | 5 |
| D.Fmr | | 1 | 3 | | D.Fmr | | 7 | 3 | 1 |
| P.Ulna | | 1 | 3 | | P.Ulna | | 1 | 8 | 2 |
| D. Rad | | 2 | 2 | | D. Rad | | 2 | 6 | 3 |
| P. Tib | | 2 | 2 | | P. Tib | | 7 | 3 | 1 |
| P. Hum | | 4 | | | P. Hum | | 11 | | |

*Fig. 13. Fusion groups for goats and sheep – Group F.*

| | Goats n=6 | | | | | Sheep n=19 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Unfused | Early Fusing | Late Fusing | Fully Fused | | Unfused | Early Fusing | Late Fusing | Fully Fused |
| P.Rad | | | | 6 | P.Rad | | | | 19 |
| Pelvis | | | | 5 | Pelvis | | | | 19 |
| Scap | | | | 6 | Scap | | | | 19 |
| D.Hum | | | | 6 | D.Hum | | | | 19 |
| 2Phl | | | | 4 | 2Phl | | | | 9 |
| 1Phl | | | | 4 | 1Phl | | | | 19 |
| D.Tib | | | 1 | 5 | D.Tib | | | | 19 |
| D.Mc | | | | 6 | D.Mc | | | | 19 |
| D.Mt | | | | 6 | D.Mt | | | | 19 |
| Rad/Ulna | | | 3 | 3 | Rad/Ulna | 14 | 5 | | |
| Calc | | | | 6 | Calc | | | 1 | 18 |
| P.Fmr(b) | | 1 | 5 | | P.Fmr(b) | | 2 | 15 | 2 |
| P.Fmr(t) | | | 2 | 4 | P.Fmr(t) | | | 3 | 16 |
| D.Fmr | | | 1 | 5 | D.Fmr | | | 10 | 9 |
| P.Ulna | | | 3 | 3 | P.Ulna | | | 5 | 14 |
| D. Rad | | | 3 | 3 | D. Rad | | | 8 | 11 |
| P. Tib | | | 2 | 4 | P. Tib | | 1 | 9 | 9 |
| P. Hum | | | 4 | 2 | P. Hum | | | 16 | 3 |

*Fig. 14. Fusion groups for goats and sheep – Group G.*

| Goats | | | | Sheep | | | |
|---|---|---|---|---|---|---|---|
| Group | Bone | Order | Estimated Age[1] | Group | Bone | Order | Estimated Age |
| A | P. Rad[2] | 1 | 0–6 | A | P. Rad | 1 | 0–6 |
| B | D. Hum | 2 | 6–12 | B | D. Hum | 2 | 6–12 |
| B | Pelvis | 2 | 6–12 | B | Pelvis | 2 | 6–12 |
| B | Scap | 2 | 6–12 | B | Scap | 2 | 6–12 |
| C | 2Phl | 3 | 12–18 | C | 2Phl | 3 | 12–18 |
| C | 1Phla | 4 | 12–18 | C | 1Phla | 4 | 12–18 |
| D | D.Tib | 5 | 18–30 | D | D.Tib | 5 | 18–30 |
| D | D.Mc | 6 | 18–30 | D | D.Mc | 6 | 18–30 |
| D | D..Mtl | 6 | 18–30 | D | D..Mtl | 6 | 18–30 |
| E | Calc | 7 | 30–48 | E | Calc | 7 | 30–48 |
| E | P.Fmr | 8 | 30–48 | E | P.Fmr | 8 | 30–48 |
| E | D.Fmr | 8 | 30–48 | E | D.Fmr | 8 | 30–48 |
| E | P.Ulna | 8 | 30–48 | E | P.Ulna | 8 | 30–48 |
| E | D.Rad | 8 | 30–48 | E | D.Rad | 9 | 30–48 |
| E | P.Tib | 8 | 30–48 | E | P.Tib | 9 | 30–48 |
| F | P. Hum [3] | 9 | 48+ | F | P. Hum | 10 | 48+ |
| G | P. Hum [4] | 10 | 48++ | G | P. Hum | 11 | 48++ |

*Fig. 15. Revised fusion sequence and ages for sheep and goats. [1] – Age in months, [2] – See fig. 4 for element abbreviations, [3] – Early fusion, [4] – Late fusion or fully fused.*

| Species | Source | P4 | M1 | M2 | M3 |
|---|---|---|---|---|---|
| 'Modern' Sheep | Silver 1969 | 21–24 | 3 | 9–12 | 18–24 |
| 'Semi-Wild' Sheep | Silver 1969 | 40 | 6 | 18 | 36–48 |
| Mixed Breeds of Sheep | Jones this volume | 24 | 3 | 10–11 | 21 |
| Mixed Breeds of Sheep | Moran and O'Connor 1974 | 23 | 2–4 | 7–12 | 17 |
| Angora Goats | Deniz and Payne 1982 | 22 | 3 | 11 | 25 |
| 'Rough' Goats | Silver 1969 | 30 | – | 12 | 30 |
| Dall Sheep (*Ovis dalli*) | Taber 1971 | 23 | 4 | 10 | 22–33 |
| Mt Goats (Oreamnos *americanus*.) | Taber 1971 | 24 | 6 | 10–16 | 16–29 |
| Himalayan Thar (*Hemitragus juemlahicus)* | Caughley 1965 | 30 | 2.5 | 11.5 | 26 |

*Fig. 16. Tooth eruption schedules for permanent teeth in months from previous studies.*

| Zeder Group | Payne Group | Age | Tooth Eruption and Wear Stages | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | dp2–3 | dp4 | P2–3 | P4 | M1 | M2 | M3 |
| I | A | 0–2m | 02–07 | 02–08 | U[1] | U | 02–03 | U | U |
| II | B | 2–6m | nd | 09–19 | U | U | 04–09 | U | U |
| III | C | 6–12m | 16–20 | 16–20 | U | U | 10–14 | 02–09 | U |
| IV | D | 1–2y | 25 | 19–25 | 02–08 | 02–08 | 13–17 | 11–14 | 02–08 |
| V | E | 2–3y | 25 | 25 | 02–08 | 02–17 | 17–19 | 11–17 | 02–11 |
| VI | F | 3–4y | S[2] | S | nd | 16–20 | 17–25 | 14317 | 12–16 |
| VII | G | 4–6y | S | S | nd | 20–25 | 18–26 | 17 | 12–17 |
| VIII | H | 6–8y | S | S | nd | 20–25 | 20–26 | 18-25 | 16–17 |
| IX | I | 8–10+y | S | S | nd | 25–26 | 25–26 | 25 | 18–26 |

*Fig. 17. Dental groups from previous studies (Payne 1973, Deniz and Payne 1982, and Zeder 1985 and 1991). [1] = U – unerupted, [2] = S – shed .*

| General Wear | Zeder 1991 | Payne (1986) | | | | Grant (1982) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | dP4 | P4 | M1&M2 | M3 | dP4 | P4 | M1&M2 | M3 |
| Eruption Stages | 02 | nye | nye | nye | nye | C | C | C | C |
| | 03 | | | | | V | V | V | V |
| | 04 | E | E | E | E | E | E | E | E |
| | 05 | ½ | ½ | ½ | ½ | H | H | H | H |
| | 06 | U | U | U | U | U | U | U | U |
| | 07 | J | J | J | J | | | | |
| | 08 | 0 | 0 | 0 | 0 | a | a | a | a |
| Early Wear | 09 | 2A | 2A | 2A | 2A | | | b | b |
| | 10 | | 4A | 4A | 4A | b | | | |
| | 11 | 5A | 5A | 5A | 5A | | | c | c |
| | 12 | 8L | | | 6G | d | | | d |
| Active Wear | 13 | | | 6A | 7G | | | d | |
| | 14 | | 7A | 7A | 8G | | e | e | e |
| | 15 | | | | 9G | | | | |
| | 16 | 13L | 8A | 8A | 10G | f | f | f | f |
| | 17 | 14L | 9A | 9A | 11G | g | g | g,h | g,h |
| Late Wear | 18 | | | 10A | 12G | | | | |
| | 19 | 16L | | 11A | 13G | h | | j | j |
| | 20 | 17L | 12S | 12A | 14G | j,k | h,j | k | k |
| | 21 | 18L | | 13A | 15G | | | | |
| | 22 | | | 14A | 16G | | | l | l |
| | 23 | 20L | | | | | | | |
| | 24 | 22L | | | | m | | | |
| Final Wear | 25 | 23L | 15A | 15A | 17G | n | l | m,n | m |
| | 26 | 23L | 1618 | 1618 | 1820 | n | | o | |

*Fig. 18. Correlation between tooth wear stages developed by Payne, Grant and Zeder.*

| Dental Group | FMNH # | Side | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| I | 112505 | L | 08 | 10 | 12 | | | | 03 | | |
| | 112505 | R | 08 | 10 | 12 | | | | 03 | | |
| III | 97916 | L | 10 | 20 | 19 | | | | 11 | 02 | |
| | 97916 | R | 10 | 20 | 19 | | | | 11 | 02 | |
| III | 97920 | L | 10 | 25 | 19 | | | | 13 | 02 | |
| | 97920 | R | 10 | 25 | 20 | | | | 13 | 02 | |
| IV | 97912 | L | 17 | 20 | 19 | | | | 14 | 07 | 02 |
| | 97912 | R | 17 | 20 | 19 | | | | 14 | 07 | 02 |
| IV | 97911 | L | 10 | 25 | 19 | | | | 16 | 05 | 02 |
| | 97911 | R | 10 | 25 | 19 | | | | 16 | 05 | 02 |
| IV | 92924 | L | 10 | 25 | 19 | 03 | 03 | 03 | 16 | 11 | 06 |
| | 92924 | R | 10 | 20 | 19 | 03 | 03 | 03 | 17 | 11 | 03 |
| V | 97908 | L | | | | 05 | 06 | 10 | 17 | 16 | 03 |
| | 97908 | R | | | | 06 | 07 | 10 | 17 | 11 | 04 |
| V | 97914 | L | | | | 09 | 10 | 11 | 17 | 13 | 04 |
| | 97914 | R | | | | 09 | 10 | 11 | 17 | 13 | 04 |
| V | 97917 | L | | | | 09 | 10 | 11 | 17 | 14 | 04 |
| | 97917 | R | | | | 09 | 10 | 11 | 17 | 14 | 04 |
| V | 97910 | L | | | | 08 | 09 | 09 | 17 | 14 | 05 |
| | 97910 | R | | | | – | 09 | 09 | 17 | 14 | 05 |
| V | 92922 | L | | | | 09 | 10 | 10 | 17 | 14 | 07 |
| | 92922 | R | | | | – | 10 | 10 | 17 | 14 | 07 |
| V | 84483 | L | | | | 09 | 10 | 14 | 17 | 16 | 05 |
| | 84483 | R | | | | 09 | 10 | 14 | 17 | 16 | 05 |
| V | 57938 | L | | | | 08 | 10 | 11 | 17 | 14 | 07 |
| | 57938 | R | | | | 08 | 10 | 11 | 17 | 16 | 07 |
| V | 84485 | L | | | | 08 | 10 | 16 | 17 | 14 | 07 |
| | 84485 | R | | | | 08 | 10 | 16 | 17 | 14 | 07 |
| V | 57253 | L | | | | 09 | 09 | 11 | 17 | 17 | 09 |
| | 57253 | R | | | | 09 | 09 | 11 | 17 | 17 | 09 |
| VI | 97913 | L | | | | 08 | 17 | 17 | 17 | 16 | 10 |
| | 97913 | R | | | | 08 | 17 | 17 | 17 | 14 | 10 |
| VI | 57937 | L | | | | 09 | 17 | 17 | 17 | 17 | 10 |
| | 57937 | R | | | | 09 | 17 | 17 | 17 | 17 | 10 |
| VII | 97919 | L | | | | 09 | 17 | 20 | 17 | 17 | 11 |
| | 97919 | R | | | | 09 | 17 | 20 | 17 | 17 | 11 |
| VII | 44472 | L | | | | 09 | 17 | 20 | 17 | 17 | 11 |
| | 44472 | R | | | | 09 | 17 | 20 | 17 | 17 | 11 |
| VII | 97925 | L | | | | 10 | 20 | 20 | 17 | 16 | 11 |
| | 97925 | R | | | | 10 | 20 | 20 | 17 | 16 | 11 |
| VII | 97921 | L | | | | 10 | 17 | 20 | 17 | 17 | 13 |
| | 97921 | R | | | | 10 | 17 | 20 | 17 | 17 | 13 |
| VII | 92921 | L | | | | 08 | 17 | 20 | 17 | 17 | 12 |
| | 92921 | R | | | | 08 | 17 | 20 | 17 | 17 | 12 |
| VII | 92923 | L | | | | 10 | 20 | 20 | 17 | 17 | 12 |
| | 92923 | R | | | | 10 | 20 | 20 | 17 | 17 | 12 |
| VII | 57949 | L | | | | 09 | 20 | 20 | 18 | 17 | 13 |
| | 57949 | R | | | | 09 | 20 | 20 | 18 | 17 | 13 |
| VII | 57935 | L | | | | 09 | 20 | 20 | 17 | 17 | 15 |
| | 57935 | R | | | | 09 | 20 | 20 | 17 | 17 | 15 |
| VIII | 97929 | L | | | | 09 | 20 | 20 | 20 | 17 | 15 |
| | 97929 | R | | | | 09 | 20 | 20 | 20 | 17 | 15 |
| VIII | 97930 | L | | | | 10 | 20 | 20 | 20 | 17 | 15 |
| | 97930 | R | | | | 10 | 20 | 20 | 20 | 17 | 15 |
| VIII | 97926 | L | | | | 10 | 20 | 20 | 19 | 17 | 17 |
| | 97926 | R | | | | 10 | 20 | 20 | 20 | 17 | 17 |
| VIII | 92925 | L | | | | 08 | 20 | 20 | 20 | 17 | 17 |
| | 92925 | R | | | | 08 | 20 | 20 | 20 | 17 | 17 |
| IX | 92920 | L | | | | 09 | 20 | 20 | 25 | 17 | 17 |
| | 92920 | R | | | | 09 | 20 | 20 | 25 | 17 | 17 |
| IX | 97924 | L | | | | 09 | 20 | 20 | 25 | 18 | 17 |
| | 97924 | R | | | | 09 | 20 | 20 | 25 | 19 | 17 |
| X | 35676 | L | | | | 17 | 20 | 25 | 25 | 17 | 17 |
| | 35676 | R | | | | 17 | 20 | 25 | 25 | 17 | 17 |
| X | 57943 | L | | | | 10 | 20 | 25 | 25 | 17 | 17 |
| | 57943 | R | | | | 10 | 20 | 20 | 25 | 18 | 17 |
| X | 99029 | L | | | | 10 | 25 | 25 | 26 | 19 | 17 |
| | 99029 | R | | | | 10 | 25 | 25 | 26 | 22 | 17 |
| XI | 58018 | L | | | | 25 | – | 26 | 26 | 26 | 22 |
| | 58018 | R | | | | 25 | 26 | 26 | 26 | 26 | 20 |

*Fig. 19. Dental eruption and wear in FMNH goats in rank order from youngest to oldest.*

| Dental Group | FMNH # | Side | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| II | 58057 | L | 10 | 10 | 16 | | | | 05 | 02 | |
| | 58057 | R | 10 | 10 | 16 | | | | 05 | 02 | |
| II | 58069 | L | 10 | 17 | 16 | | | | 09 | 02 | |
| | 58069 | R | 10 | 17 | 16 | | | | 09 | 02 | |
| II | 58072 | L | 10 | 20 | 17 | | | | 07 | | |
| | 58072 | R | 10 | 20 | 17 | | | | 07 | | |
| III | 97986 | L | 17 | 25 | 19 | | | | 11 | 02 | |
| | 97986 | R | 17 | 25 | 19 | | | | 11 | 02 | |
| III | 97959 | L | 20 | 25 | 19 | | | | 14 | 03 | |
| | 97959 | R | 20 | 25 | 19 | | | | 14 | 03 | |
| IV | 58039 | L | 17 | 20 | 19 | | | | 13 | 08 | 02 |
| | 58039 | R | 17 | 20 | 17 | | | | 11 | 08 | 02 |
| IV | 58094 | L | 17 | 25 | 17 | | | | 16 | 05 | 02 |
| | 58094 | R | 17 | 25 | 17 | | | | 16 | 05 | 02 |
| IV | 58020 | L | 20 | 25 | 21 | | | | 14 | 09 | 02 |
| | 58020 | R | 20 | 25 | 21 | | | | 14 | 09 | 02 |
| IV | 57254 | L | 20 | 25 | 19 | | | | 16 | 07 | 02 |
| | 57254 | R | 20 | 25 | 19 | | | | 17 | 07 | 02 |
| IV | 84488 | L | 25 | 26 | 19 | | | | 16 | 05 | 02 |
| | 84488 | R | – | 26 | 19 | | | | 16 | 05 | 02 |
| IV | 58022 | L | 20 | 25 | 19 | | | | 17 | 08 | 02 |
| | 58022 | R | – | 25 | 19 | | | | 17 | 09 | 02 |
| IV | 58024 | L | 10 | 25 | 25 | | | | 17 | 11 | 02 |
| | 58024 | R | 10 | 25 | 25 | | | | 17 | 11 | 02 |
| V | 58040 | L | | | | – | 10 | 10 | 17 | 13 | 07 |
| | 58040 | R | | | | – | 10 | 10 | 17 | 13 | 07 |
| V | 58063 | L | | | | 09 | 10 | 11 | 17 | 14 | 09 |
| | 58063 | R | | | | 09 | 10 | 11 | 17 | 14 | 09 |
| V | 58021 | R | | | | 08 | 08 | 09 | 17 | 16 | 07 |
| V | 58065 | L | | | | 09 | 10 | 16 | 17 | 14 | 10 |
| | 58065 | R | | | | 09 | 10 | 14 | 17 | 14 | 10 |
| V | 58038 | L | | | | 08 | 10 | 10 | 17 | 14 | 05 |
| | 58038 | R | | | | 08 | 10 | 10 | 17 | 14 | 05 |
| V | 58014 | L | | | | – | 10 | 16 | 17 | 14 | 05 |
| | 58014 | R | | | | – | – | 16 | 17 | 16 | 05 |
| V | 58091 | L | | | | 09 | 10 | 11 | 17 | 14 | 10 |
| | 58091 | R | | | | 09 | 10 | 11 | 17 | 14 | 10 |
| V | 58047 | L | | | | 09 | 09 | 11 | 17 | 16 | 09 |
| | 58047 | R | | | | 09 | 09 | 11 | 17 | 16 | 09 |
| V | 152003 | L | | | | 08 | 09 | 10 | 17 | 16 | 09 |
| | 152003 | R | | | | 08 | 10 | 10 | 17 | 16 | 10 |
| V | 58058 | L | | | | 08 | 09 | 11 | 17 | 16 | 10 |
| | 58058 | R | | | | 08 | 09 | 11 | 17 | 16 | 10 |
| V | 58033 | L | | | | 08 | 17 | 14 | 17 | 16 | 07 |
| | 58033 | R | | | | 08 | 16 | 14 | 17 | 16 | 07 |
| VI | 97984 | L | | | | 08 | 17 | 17 | 17 | 14 | 09 |
| | 97984 | R | | | | 08 | 10 | 17 | 17 | 14 | 09 |
| VI | 97960 | L | | | | 08 | 10 | 17 | 17 | 14 | 10 |
| | 97960 | R | | | | 08 | 10 | 17 | 17 | 14 | 10 |
| VI | 58044 | L | | | | 10 | 17 | 17 | 17 | 16 | 10 |
| | 58044 | R | | | | 10 | 17 | 17 | 17 | 14 | 10 |
| VI | 97958 | L | | | | 09 | 10 | 16 | 17 | 14 | 11 |
| | 97958 | R | | | | 09 | 10 | 16 | 17 | 16 | 11 |
| VI | 57255 | L | | | | – | 10 | 16 | 17 | 17 | 11 |
| | 57255 | R | | | | 08 | 10 | 16 | 17 | 17 | 11 |
| VI | 98162 | L | | | | – | 10 | 17 | 17 | 17 | 09 |
| | 98162 | R | | | | 09 | 10 | 17 | 17 | 17 | 09 |
| VI | 97985 | L | | | | 08 | 17 | 17 | 17 | 16 | 09 |
| | 97985 | R | | | | 08 | 17 | 17 | 17 | 16 | 09 |
| VI | 58032 | L | | | | – | 10 | 17 | 17 | 16 | 11 |
| | 58032 | R | | | | – | 10 | 17 | 17 | 16 | 11 |
| VI | 58019 | L | | | | 09 | 17 | 17 | 17 | 17 | 11 |
| | 58019 | R | | | | 10 | 17 | 17 | 17 | 16 | 10 |
| VI | 58037 | L | | | | – | 17 | 17 | 17 | 17 | 12 |
| | 58037 | R | | | | 09 | 17 | 17 | 17 | 17 | 12 |

*Fig. 20. Dental eruption and wear in FMNH sheep in rank order from youngest to oldest.*

| Dental Group | FMNH # | Side | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **VI** | 98161 | L | | | | 09 | 17 | 17 | 17 | 17 | 15 |
| | 98161 | R | | | | 09 | 17 | 17 | 17 | 17 | 15 |
| **VI** | 97957 | L | | | | 10 | 17 | 17 | 17 | 17 | 16 |
| | 97957 | R | | | | 10 | 17 | 17 | 17 | 17 | 16 |
| **VII** | 58089 | L | | | | 09 | 14 | 14? | 17 | 17 | 15 |
| | 58089 | R | | | | 09 | 17 | 20 | 17 | 17 | 15 |
| **VII** | 58048 | L | | | | 10 | 17 | 20 | 17 | 17 | 14 |
| | 58048 | R | | | | 10 | 17 | 20 | 17 | 17 | 14 |
| **VII** | 58034 | L | | | | – | 17 | 20 | 17 | 17 | 15 |
| | 58034 | R | | | | 10 | 17 | 20 | 17 | 17 | 15 |
| **VII** | 58042 | L | | | | 09 | 17 | – | 17 | 17 | 14 |
| | 58042 | R | | | | – | 17 | 20 | 17 | 17 | 16 |
| **VII** | 58070 | L | | | | 17 | 20 | 20 | 17 | 17 | 17 |
| | 58070 | R | | | | 17 | 20 | 20 | 17 | 17 | 17 |
| **VII** | 97983 | L | | | | 20 | 20 | 17 | 17 | 17 | 17 |
| | 97983 | R | | | | 20 | 20 | 17 | 17 | 17 | 16 |
| **VII** | 58035 | L | | | | 17 | 20 | 17 | 18 | 17 | 17 |
| | 58035 | R | | | | 17 | 20 | 17 | 18 | 17 | 17 |
| **VII** | 58043 | L | | | | 10 | 20 | 20 | 19 | 17 | 17 |
| | 58043 | R | | | | 10 | 20 | 17 | 18 | 17 | 17 |
| **VIII** | 152005 | L | | | | 20 | 25 | 20 | 20 | 17 | 16 |
| | 152005 | R | | | | 20 | 25 | 17 | 19 | 17 | 15 |
| **VIII** | 97973 | L | | | | 10 | 17 | 20 | 20 | 17 | 17 |
| | 97973 | R | | | | 09 | 17 | 20 | 20 | 17 | 17 |
| **IX** | 58062 | L | | | | 10 | 17 | 20 | 22 | 17 | 17 |
| | 58062 | R | | | | 10 | 17 | 20 | 22 | 17 | 17 |
| **IX** | 58071 | L | | | | 10 | 20 | 20 | 25 | 17 | 16 |
| | 58071 | R | | | | 10 | 20 | 20 | 25 | 17 | 16 |
| **IX** | 58036 | L | | | | – | 20 | 20 | 25 | 17 | 17 |
| | 58036 | R | | | | 20 | 25 | 20 | 25 | 17 | 17 |
| **IX** | 58031 | L | | | | 17 | 20 | 20 | 25 | 18 | 18 |
| | 58031 | R | | | | – | 20 | 20 | 22 | 18 | 18 |
| **X** | 58064 | L | | | | 20 | 20 | 22 | 25 | 18 | 17 |
| | 58064 | R | | | | 20 | 20 | 22 | 25 | 18 | 17 |
| **X** | 58045 | L | | | | – | 25 | 26 | 26 | 18 | 17 |
| | 58045 | R | | | | 20 | 25 | 26 | 26 | 19 | 17 |
| **X** | 92928 | L | | | | 25 | 25 | 26 | 25 | 22 | 17 |
| | 92928 | R | | | | 25 | 25 | 26 | 25 | 18 | 17 |
| **XI** | 58015 | L | | | | 25 | 25 | 25 | 25 | 22 | 17 |
| | 58015 | R | | | | 25 | 25 | 25 | 25 | 25 | 18 |
| **XII** | 58041 | L | | | | 10 | 25 | 20 | 26 | 26 | 26 |
| | 58041 | R | | | | – | 25 | 20 | – | – | 26 |

*Fig. 20. continued.*

| Group I | Goats n=1 | | | | | | | | | Group II | Sheep n=3 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | 2 | |
| **03** | | | | | | | 1 | | | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | 1 | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | 1 | | |
| **08** | 1 | | | | | | | | | **08** | | | | | | | | | |
| **09** | | | | | | | | | | **09** | | | | | | | 1 | | |
| **10** | | 1 | | | | | | | | **10** | 3 | 1 | | | | | | | |
| **11** | | | 1 | | | | | | | **11** | | | | | | | | | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | | | | **13** | | | | | | | | | |
| **14** | | | | | | | | | | **14** | | | | | | | | | |
| **15** | | | | | | | | | | **15** | | | | | | | | | |
| **16** | | | | | | | | | | **16** | | | 1 | | | | | | |
| **17** | | | | | | | | | | **17** | | 1 | 1 | | | | | | |
| **18** | | | | | | | | | | **18** | | | | | | | | | |
| **19** | | | | | | | | | | **19** | | | | | | | | | |
| **20** | | | | | | | | | | **20** | | 1 | | | | | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | | | | | | | **25** | | | | | | | | | |
| **26** | | | | | | | | | | **26** | | | | | | | | | |

*Fig. 21. Dental groups for FMNH goats and sheep – Groups I and II.*

| Group III | Goats n= 2 | | | | | | | | | Group III | Sheep n=2 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | 2 | | **02** | | | | | | | | 1 | |
| **03** | | | | | | | | | | **03** | | | | | | | | 1 | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | | | |
| **08** | | | | | | | | | | **08** | | | | | | | | | |
| **09** | | | | | | | | | | **09** | | | | | | | | | |
| **10** | 2 | | | | | | | | | **10** | | | | | | | | | |
| **11** | | | | | | | 1 | | | **11** | | | | | | | 1 | | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | 1 | | | **13** | | | | | | | | | |
| **14** | | | | | | | | | | **14** | | | | | | | 1 | | |
| **15** | | | | | | | | | | **15** | | | | | | | | | |
| **16** | | | | | | | | | | **16** | | | | | | | | | |
| **17** | | | | | | | | | | **17** | 1 | | | | | | | | |
| **18** | | | | | | | | | | **18** | | | | | | | | | |
| **19** | | | 1 | | | | | | | **19** | | | 2 | | | | | | |
| **20** | | 1 | 1 | | | | | | | **20** | 1 | | | | | | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | 1 | | | | | | | | **25** | | 2 | | | | | | | |
| **26** | | | | | | | | | | **26** | | | | | | | | | |

*Fig. 22. Dental groups for FMNH goats and sheep – Group III.*

| Group IV | Goats n= 3 | | | | | | | | | Group IV | Sheep n=7 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | 2 | **02** | | | | | | | | | 7 |
| **03** | | | | 1 | 1 | 1 | | | 1.5 | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | 2 | |
| **06** | | | | | | | | 1 | 1.5 | **06** | | | | | | | | | |
| **07** | | | | | | | | 1 | | **07** | | | | | | | | 1 | |
| **08** | | | | | | | | | | **08** | | | | | | | | 1.5 | |
| **09** | | | | | | | | | | **09** | | | | | | | | 1.5 | |
| **10** | 2 | | | | | | | | | **10** | 1 | | | | | | | | |
| **11** | | | | | | | | 1 | | **11** | | | | | | | .5 | 1 | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | | | | **13** | | | | | | | .5 | | |
| **14** | | | | | | | 1 | | | **14** | | | | | | | 1 | | |
| **15** | | | | | | | | | | **15** | | | | | | | | | |
| **16** | | | | | | | 1.5 | | | **16** | | | | | | | 2.5 | | |
| **17** | 1 | | | | | | 1.5 | | | **17** | 2 | | 1.5 | | | | 2.5 | | |
| **18** | | | | | | | | | | **18** | | | | | | | | | |
| **19** | | | 3 | | | | | | | **19** | | | 3.5 | | | | | | |
| **20** | | 1.5 | | | | | | | | **20** | 2.5 | 1 | | | | | | | |
| **21** | | | | | | | | | | **21** | | | 1 | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | 1.5 | | | | | | | | **25** | .5 | 5 | 1 | | | | | | |
| **26** | | | | | | | | | | **26** | | 1 | | | | | | | |

*Fig. 23. Dental groups for FMNH goats and sheep – Group IV.*

| Group V | Goats n= 9 | | | | | | | | | Group V | Sheep n=11 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | | |
| **03** | | | | | | | | | .5 | **03** | | | | | | | | | |
| **04** | | | | | | | | | 2.5 | **04** | | | | | | | | | |
| **05** | | | | .5 | | | | | 2 | **05** | | | | | | | | | 2 |
| **06** | | | | .5 | .5 | | | | | **06** | | | | | | | | | |
| **07** | | | | | .5 | | | | 3 | **07** | | | | | | | | | 2.5 |
| **08** | | | | 2.5 | | | | | | **08** | | | | 4.5 | | | | | |
| **09** | | | | 4.5 | 2 | 1 | | | 1 | **09** | | | | 4 | | .5 | | | 2.5 |
| **10** | | | | | 6 | 2 | | | | **10** | | | | | 5.5 | 3 | | | 3.5 |
| **11** | | | | | | 4 | | .5 | | **11** | | | | | | 4 | | | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | | 1 | | **13** | | | | | | | | 1 | |
| **14** | | | | | | 1 | | 4.5 | | **14** | | | | | | 1.5 | | 4 | |
| **15** | | | | | | | | | | **15** | | | | | | | | | |
| **16** | | | | | | 1 | | 2 | | **16** | | | | | .5 | 1.5 | | 4 | |
| **17** | | | | | | | 9 | 1 | | **17** | | | | | .5 | | 10.5 | | |
| **18** | | | | | | | | | | **18** | | | | | | | | | |
| **19** | | | | | | | | | | **19** | | | | | | | | | |
| **20** | | | | | | | | | | **20** | | | | | | | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | | | | | | | **25** | | | | | | | | | |
| **26** | | | | | | | | | | **26** | | | | | | | | | |

*Fig. 24. Dental groups for FMNH goats and sheep – Group V.*

| Group VI | Goats n= 2 | | | | | | | | | Group VI | Sheep n=12 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | | |
| **03** | | | | | | | | | | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | | | |
| **08** | | | | 1 | | | | | | **08** | | | | 3.5 | | | | | |
| **09** | | | | 1 | | | | | | **09** | | | | 3.5 | | | | | 3 |
| **10** | | | | | | | | | 2 | **10** | | | | 2.5 | 5.5 | | | | 2.5 |
| **11** | | | | | | | | | | **11** | | | | | | | | | 3.5 |
| **12** | | | | | | | | | | **12** | | | | | | | | | 1 |
| **13** | | | | | | | | | | **13** | | | | | | | | | |
| **14** | | | | | | | | .5 | | **14** | | | | | | | | 3 | |
| **15** | | | | | | | | | | **15** | | | | | | | | | 1 |
| **16** | | | | | | | | .5 | | **16** | | | | | | 2 | | 3.5 | 1 |
| **17** | | | | | 2 | 2 | 2 | 1 | | **17** | | | | | 6.5 | 10 | 12 | 5.5 | |
| **18** | | | | | | | | | | **18** | | | | | | | | | |
| **19** | | | | | | | | | | **19** | | | | | | | | | |
| **20** | | | | | | | | | | **20** | | | | | | | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | | | | | | | **25** | | | | | | | | | |
| **26** | | | | | | | | | | **26** | | | | | | | | | |

*Fig. 25. Dental groups for FMNH goats and sheep – Group VI.*

| Group VII | Goats n= 8 | | | | | | | | | Group VII | Sheep n=8 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | | |
| **03** | | | | | | | | | | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | | | |
| **08** | | | | 1 | | | | | | **08** | | | | | | | | | |
| **09** | | | | 4 | | | | | | **09** | | | | 1.5 | | | | | |
| **10** | | | | 3 | | | | | | **10** | | | | 2.5 | | | | | |
| **11** | | | | | | | | | 3 | **11** | | | | | | | | | |
| **12** | | | | | | | | | 2 | **12** | | | | | | | | | |
| **13** | | | | | | | | | 2 | **13** | | | | | | | | | |
| **14** | | | | | | | | | | **14** | | | | | .5 | .5 | | | 1.5 |
| **15** | | | | | | | | | 1 | **15** | | | | | | | | | 2 |
| **16** | | | | | | | | 1 | | **16** | | | | | | | | | 1 |
| **17** | | | | | 4 | | 7 | 7 | | **17** | | | | | 3.5 | 2.5 | 6 | 8 | 3.5 |
| **18** | | | | | | | 1 | | | **18** | | | | | | | 1.5 | | |
| **19** | | | | | | | | | | **19** | | | | | | | .5 | | |
| **20** | | | | | 4 | 8 | | | | **20** | | | | | 4 | 4.5 | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | | | | | | | **25** | | | | | | | | | |
| **26** | | | | | | | | | | **26** | | | | | | | | | |

*Fig. 26. Dental groups for FMNH goats and sheep – Group VII.*

| Group VIII | Goats n= 4 | | | | | | | | | Group VIII | Sheep n=2 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | | |
| **03** | | | | | | | | | | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | | | |
| **08** | | | | 1 | | | | | | **08** | | | | | | | | | |
| **09** | | | | 1 | | | | | | **09** | | | | .5 | | | | | |
| **10** | | | | 2 | | | | | | **10** | | | | .5 | | | | | |
| **11** | | | | | | | | | | **11** | | | | | | | | | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | | | | **13** | | | | | | | | | |
| **14** | | | | | | | | | | **14** | | | | | | | | | |
| **15** | | | | | | | | | 2 | **15** | | | | | | | | | .5 |
| **16** | | | | | | | | | | **16** | | | | | | | | | .5 |
| **17** | | | | | | | | 4 | 2 | **17** | | | | | 1 | 1 | | 2 | 1 |
| **18** | | | | | | | | | | **18** | | | | | | | .5 | | |
| **19** | | | | | | | .5 | | | **19** | | | | | | | .5 | | |
| **20** | | | | | 4 | 4 | 3.5 | | | **20** | | | | 1 | | 1 | 1.5 | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | | | | | | | **25** | | | | | 1 | | | | |
| **26** | | | | | | | | | | **26** | | | | | | | | | |

*Fig. 27. Dental groups for FMNH goats and sheep – Group VIII.*

| Group IX | Goats n= 2 | | | | | | | | | Group IX | Sheep n=4 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | | |
| **03** | | | | | | | | | | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | | | |
| **08** | | | | | | | | | | **08** | | | | | | | | | |
| **09** | | | | 2 | | | | | | **09** | | | | | | | | | |
| **10** | | | | | | | | | | **10** | | | | 2 | | | | | |
| **11** | | | | | | | | | | **11** | | | | | | | | | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | | | | **13** | | | | | | | | | |
| **14** | | | | | | | | | | **14** | | | | | | | | | |
| **15** | | | | | | | | | | **15** | | | | | | | | | |
| **16** | | | | | | | | | | **16** | | | | | | | | | 1 |
| **17** | | | | | | | | 1 | 2 | **17** | | | | .5 | 1 | | | 3 | 2 |
| **18** | | | | | | | | .5 | | **18** | | | | | | | | 1 | 1 |
| **19** | | | | | | | | .5 | | **19** | | | | | | | | | |
| **20** | | | | | 2 | 2 | | | | **20** | | | | .5 | 2.5 | 4 | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | | **22** | | | | | | | 1.5 | | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | | | | 2 | | | **25** | | | | | .5 | | 2.5 | | |
| **26** | | | | | | | | | | **26** | | | | | | | | | |

*Fig. 28. Dental groups for FMNH goats and sheep – Group IX.*

| Group X | Goats n= 3 | | | | | | | | | Group X | Sheep n=3 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | | |
| **03** | | | | | | | | | | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | | | |
| **08** | | | | | | | | | | **08** | | | | | | | | | |
| **09** | | | | 2 | | | | | | **09** | | | | | | | | | |
| **10** | | | | | | | | | | **10** | | | | | | | | | |
| **11** | | | | | | | | | | **11** | | | | | | | | | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | | | | **13** | | | | | | | | | |
| **14** | | | | | | | | | | **14** | | | | | | | | | |
| **15** | | | | | | | | | | **15** | | | | | | | | | |
| **16** | | | | | | | | | | **16** | | | | | | | | | |
| **17** | | | | 1 | | | | 1.5 | 3 | **17** | | | | | | | | | 3 |
| **18** | | | | | | | | .5 | | **18** | | | | | | | | 2 | |
| **19** | | | | | | | | .5 | | **19** | | | | | | | | .5 | |
| **20** | | | | | 2 | .5 | | | | **20** | | | | 1.5 | 1 | | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | .5 | | **22** | | | | | | 1 | | | |
| **23** | | | | | | | | | | **23** | | | | | | | | .5 | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | | 1 | 2.5 | 2 | | | **25** | | | | 1 | 2 | | 2 | | |
| **26** | | | | | | | 1 | | | **26** | | | | | | 2 | 1 | | |

*Fig. 29. Dental groups for FMNH goats and sheep – Group X.*

| Group XI | Goats n= 1 | | | | | | | | | Group XI XII | Sheep n=2 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 | | dP2 | dP3 | dP4 | P2 | P3 | P4 | M1 | M2 | M3 |
| **02** | | | | | | | | | | **02** | | | | | | | | | |
| **03** | | | | | | | | | | **03** | | | | | | | | | |
| **04** | | | | | | | | | | **04** | | | | | | | | | |
| **05** | | | | | | | | | | **05** | | | | | | | | | |
| **06** | | | | | | | | | | **06** | | | | | | | | | |
| **07** | | | | | | | | | | **07** | | | | | | | | | |
| **08** | | | | | | | | | | **08** | | | | | | | | | |
| **09** | | | | | | | | | | **09** | | | | | | | | | |
| **10** | | | | | | | | | | **10** | | | | | | | | | |
| **11** | | | | | | | | | | **11** | | | | | | | | | |
| **12** | | | | | | | | | | **12** | | | | | | | | | |
| **13** | | | | | | | | | | **13** | | | | | | | | | |
| **14** | | | | | | | | | | **14** | | | | | | | | | |
| **15** | | | | | | | | | | **15** | | | | | | | | | |
| **16** | | | | | | | | | | **16** | | | | | | | | | |
| **17** | | | | | | | | | | **17** | | | | .5 | | | | | .5 |
| **18** | | | | | | | | | | **18** | | | | | | | | | .5 |
| **19** | | | | | | | | | | **19** | | | | | | | | | |
| **20** | | | | | | | | | .5 | **20** | | | | | | 1 | | | |
| **21** | | | | | | | | | | **21** | | | | | | | | | |
| **22** | | | | | | | | | .5 | **22** | | | | | | | | .5 | |
| **23** | | | | | | | | | | **23** | | | | | | | | | |
| **24** | | | | | | | | | | **24** | | | | | | | | | |
| **25** | | | | 1 | | | | | | **25** | | | | 1 | 2 | 1 | 1 | .5 | |
| **26** | | | | | 1 | 1 | 1 | 1 | | | | | | | | | .5 | .5 | 1 |

*Fig. 30. Dental groups for FMNH goats and sheep – Group XI and XII*

| Revised Group | Zeder Group | Payne Group | Age | Tooth Eruption and Wear Stages | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | dp2 | dp3 | dp4 | P2 | P3 | P4 | M1 | M2 | M3 |
| I | I | A | 0–2m | 08 | 10 | 11 | U | U | U | 03 | U | U |
| II | II | B | 2–6m | – | – | – | – | 3 | – | – | – | – |
| III | III | C | 6–12m | 10 | 20–25 | 19-20 | U | U | U | 11–13 | 02 | U |
| IV | IV | D | 12–18m | 10–17 | 20–25 | 19 | U–03 | U–03 | U–03 | 14–17 | 06–11 | 02–06 |
| V | IV | D | 18–24m | S | S | S | 05–09 | 06–10 | 09–16 | 17 | 11–17 | 03–09 |
| VI | V | E | 2–3y | S | S | S | 08–09 | 17 | 17 | 17 | 14–17 | 10 |
| VII | VI | F | 3–4y | S | S | S | 08–10 | 17–20 | 20 | 17–18 | 16–17 | 11–15 |
| VIII | VII | G | 4–5y | S | S | S | 08–10 | 20 | 20 | 19–20 | 17 | 15–17 |
| IX | VII | G | 5–6y | S | S | S | 09 | 20 | 20 | 25 | 17–19 | 17 |
| X | VIII | H | 6–8y | S | S | S | 09-17 | 20–25 | 20–25 | 25–26 | 17–22 | 17 |
| XI | IX | I | 8–10y | S | S | S | 25 | 26 | 26 | 26 | 26 | 20–23 |
| XII | IX | I | 10+ | – | – | – | – | – | – | – | – | – |

*Fig. 31. Revised dental groups for goats.*

| Revised Group | Zeder Group | Payne Group | Age | Tooth Eruption and Wear Stages | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | dp2 | dp3 | dp4 | P2 | P3 | P4 | M1 | M2 | M3 |
| I | I | A | 0–2m | – | – | – | – | – | – | – | – | – |
| II | II | B | 2–6m | 10 | 10–20 | 16–17 | U | U | U | 04–09 | 02 | U |
| III | III | C | 6–12m | 17–20 | 25 | 19 | U | U | U | 11–14 | 02–03 | U |
| IV | IV | D | 12–18m | 10–25 | 20–26 | 17–25 | U | U | U | 11–17 | 05–10 | 02 |
| V | IV | D | 18–24m | S | S | S | 08–09 | 10–17 | 09–16 | 17 | 13–16 | 05–10 |
| VI | V | E | 2–3y | S | S | S | 08–10 | 10–17 | 16–17 | 17 | 14–17 | 09–16 |
| VII | VI | F | 3–4y | S | S | S | 09–10 | 14–20 | 14–20 | 17–19 | 17 | 14–17 |
| VIII | VII | G | 4–5y | S | S | S | 09–20 | 17–25 | 17–20 | 18–20 | 17 | 15–17 |
| IX | VII | G | 5–6y | S | S | S | 10–20 | 17–25 | 20 | 22–25 | 17–18 | 16–18 |
| X | VIII | H | 6–8y | S | S | S | 20–25 | 20–25 | 22–26 | 25–26 | 18–23 | 17 |
| XI | IX | I | 8–10y | S | S | S | 25 | 25 | 25 | 25 | 22–25 | 17–18 |
| XII | IX | I | 10+y | S | S | S | 10 | 25 | 20 | 26 | 26 | 26 |

*Fig. 32. Revised dental groups for sheep.*

| Goats | A 0-6m | B 6-12m | C 12-18m | D 18-30m | E 30-48m | F 48+m | G 18++m | Sheep | A 0-6m | B 6-12m | C 12-18m | D 18-30m | E 30-48m | F 48+m | G 18++m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **I 0-2m** | | | | | | | | **I 0-2m** | | | | | | | |
| **II 2-6m** | | | | | | | | **II 2-6m** | 1 | 2 | | | | | |
| **III 6-12m** | 2 | | | | | | | **III 6-12m** | | 1 | 1 | | | | |
| **IV 12-18m** | | 2 | 1 | | | | | **IV 12-18m** | | | 5 | 2 | | | |
| **V 18-24m** | | | 4 | 5 | | | | **V 18-24m** | | | | 4 | 4 | 3 | |
| **VI 24-36m** | | | | 2 | | | | **VI 24-36m** | | | | 4 | 5 | 2 | 1 |
| **VII 36-48m** | | | | | 5 | 1 | 1 | **VII 36-48m** | | | | | | 4 | 4 |
| **VIII 4-5y** | | | | 2 | 1 | 1 | | **VIII 4-5y** | | | | | | | 2 |
| **IX 5-6y** | | | | | 1 | 1 | | **IX 5-6y** | | | | | | | 3 |
| **X 6-8y** | | | | | 1 | | 2 | **X 6-8y** | | | | | | | 3 |
| **XI 8-10y** | | | | | | | 1 | **XI 8-10y** | | | | | | | 1 |
| **XII 10+y** | | | | | | | | **XII 10+y** | | | | | | | 1 |

*Fig. 33. Correlation between fusion and dental groups for goats and sheep (dental group dark shading indicates exact overlap in estimated ages, light shading indicates overlap with either the beginning or end of age range).*

| Males | A 0–6m | B 6–12m | C 12–18m | D 18–30m | E 30–48m | F 48+m | G 18++m | Females | A 0–6m | B 6–12m | C 12–18m | D 18–30m | E 30–48m | F 48+m | G 18++m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I 0–2m | | | | | | | | I 0–2m | | | | | | | |
| II 2–6m | | | | | | | | II 2–6m | | | | | | | |
| III 6–12m | 2 | | | | | | | III 6–12m | | 2 | | | | | |
| IV 12–18m | | | 1 | | | | | IV 12–18m | | | | | | | |
| V 18–24m | | | 4 | 2 | | | | V 18–24m | | | | 2 | | | |
| VI 24–36m | | | | 2 | | | | VI 24–36m | | | | | | | |
| VII 36–48m | | | | 1 | | | | VII 36–48m | | | | | 5 | 1 | 1 |
| VIII 4–5y | | | | 1 | 1 | | | VIII 4–5y | | | | 1 | | 1 | |
| IX 5–6y | | | | | | 1 | | IX 5–6y | | | | | 1 | | |
| X 6–8y | | | | | 1 | | 1 | X 6–8y | | | | | | | 1 |
| XI 8–10y | | | | | | | | XI 8–10y | | | | | | | |
| XII 10+y | | | | | | | 1 | XII 10+y | | | | | | | |

*Fig. 34. Correlation between fusion and dental groups for male and female goats (dental group dark shading indicates exact overlap in estimated ages, light shading indicates overlap with either the beginning or end of age range).*

| Males | A 0–6m | B 6–12m | C 12–18m | D 18–30m | E 30–48m | F 48+m | G 18++m | Females | A 0–6m | B 6–12m | C 12–18m | D 18–30m | E 30–48m | F 48+m | G 18++m |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I 0–2m | | | | | | | | I 0–2m | | | | | | | |
| II 2–6m | 1 | | | | | | | II 2–6m | | 2 | | | | | |
| III 6–12m | | | | | | | | III 6–12m | | 1 | 1 | | | | |
| IV 12–18m | | | 4 | | | | | IV 12–18m | | | 1 | 2 | | | |
| V 18–24m | | | | 4 | | | | V 18–24m | | | | | 4 | 3 | |
| VI 24–36m | | | | 4 | 3 | 1 | | VI 24–36m | | | | | 2 | 1 | 1 |
| VII 36–48m | | | | | | 3 | 2 | VII 36–48m | | | | | | 1 | 2 |
| VIII 4–5y | | | | | | | 1 | VIII 4–5y | | | | | | | 1 |
| IX 5–6y | | | | | | | 2 | IX 5–6y | | | | | | | 2 |
| X 6–8y | | | | | | | 1 | X 6–8y | | | | | | | 2 |
| XI 8–10y | | | | | | | | XI 8–10y | | | | | | | 1 |
| XII 10+y | | | | | | | 1 | XII 10+y | | | | | | | |

*Fig. 35. Correlation between fusion and dental groups for male and female sheep (dental group dark shading indicates exact overlap in estimated ages, light shading indicates overlap with either the beginning or end of age range).*

*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 119–128*

# 7. Accuracy of Age Determinations from Tooth Crown Heights: a Test Using an Expanded Sample of Known Age Red Deer (*Cervus elaphus*)

*T. E. Steele*

*The utility of the Quadratic Crown Height Method (QCHM) for estimating animal age-at-death from hypsodont ungulate teeth was tested using a sample of known-age Rocky Mountain elk (*Cervus elaphus*) from western Montana. There is no difference in wear rate between males and females, so the sample can be analyzed in its entirety. Regression of age on lower first molar crown height (n = 163) shows that there is a good relationship between crown height and age, and regression equations can satisfactorily estimate age from crown height in specimens from the population that provided the known-age individuals. However, fixed regression equations can only adequately estimate age in samples whose teeth are the same size as the known-age sample, and* C. elaphus *body and tooth size varies in time and space. Therefore, flexible equations such as those from the QCHM are desirable, but the QCHM did not adequately estimate age in the known-age sample. I adjusted the formula by changing the age of potential ecological longevity to the age of the tooth's longevity, and I confirmed that the quadratic curve best fits the data for lower first molars. I also compared the relationship between crown height and age in* C. elaphus *to the relationship found in known-age samples of* Odocoileus virginianus *and* Rangifer tarandus.

## Introduction

Faunal analysts have long recognized that the age distribution of a species in a sample provides data about the species' life history patterns and the specimens' depositional history, but assigning specimens into age classes is not always easy. Numerous methods exist for assessing age-at-death of archaeological specimens (papers in this volume, Amorosi 1989; Morris 1972; Pike-Tay 2000; Wilson, Grigson, and Payne 1982), but epiphyseal fusion, tooth cementum annuli, and tooth development, eruption, and wear remain the most frequently applied methods (for summaries see Klein and Cruz-Uribe 1984; O'Connor 2000; Reitz and Wing 1999). Methods based on tooth eruption and wear are most frequently used, because they monitor age throughout an animal's life, not just during growth (e.g. epiphyseal fusion) and because they are non-destructive and do not require specialized technical skill and equipment (e.g. counting cementum annuli). Wear often is documented by coding stages, but many researchers have utilized metric measurements of tooth crown height. Measurements are preferable to coded stages because they are replicable, easy to apply to isolated teeth, and more amenable to quantitative analyses. While raw measurements can be directly compared, often measurements are used with equations that can estimate age-at-death in months. This study assesses the utility of the Quadratic Crown Height Method (QCHM), which is a set of flexible formulae that can be used to estimate age-at-death from tooth crown heights.

## The Known-Age Sample

In order to investigate the relationship between crown height and age, I used a sample of Rocky Mountain elk (*Cervus elaphus*, Linnaeus 1758) mandibles from western Montana just north of Yellowstone National Park, Wyoming in the United States. These specimens originate from individuals that were marked as calves and were

subsequently retrieved at hunter checkpoints, and therefore have known age-at-death (in months) and, in most cases, known sex. This sample was created from two sources. One source was the mandibles collected by Quimby and Gaab (1957) for their wear-stage study (housed by the Fish and Wildlife Management Program, Montana State University-Bozeman). C. Wolf measured tooth crown heights on 170 specimens from this sample, and these measurements were used by Klein and colleagues (Klein, Allwarden, and Wolf 1983; Klein and Cruz-Uribe 1983; Klein *et al.* 1981) in their studies of the relationship between tooth crown height and age. These measurements are also used here. The second source of known-age specimens was collected by Hamlin *et al.* (2000) to compare estimates of age using wear stages to those based on incisor cementum annuli (housed by the Montana Department of Fish, Wildlife, and Parks-Bozeman). I measured tooth crown heights on 56 of these mandibles. The mean inter-observer error for tooth crown height measurements is low at n = 110, 2.9%, 0.24 mm (Steele 2002, 167; see also Morrison and Whitridge 1997), thus measurements can be combined. C. Wolf's 170 specimens plus my 56 mandibles brings the known-age sample to 226 individuals (Fig. 1, male: n = 79, female: n = 129, unknown: n = 18). Although most of the specimens are still under 72 months (6 years), this expanded sample increases the number of individuals in the 78–104 months (6.5–8.5 years) age category from what was available in previous studies. The oldest age classes are still underrepresented, because these animals are rare in most mammal populations (Caughley 1966; Deevey 1947). The older individuals in this sample are primarily females, because adult males are less numerous in the population due to extermination earlier in life by human hunters (K. Hamlin, pers. comm.).

| *age cohorts years (months)* | *total* | *m1* | *males (m1)* | *females (m1)* |
|---|---|---|---|---|
| 0.5 (5–10) | 42 | | | |
| 1.5 (17–20) | 41 | 21 | 9 | 11 |
| 2.5 (27–33) | 36 | 36 | 15 | 15 |
| 3.5 (40–44) | 33 | 33 | 7 | 23 |
| 4.5 (53–57) | 25 | 25 | 6 | 17 |
| 5.5 (65–68) | 15 | 15 | 4 | 9 |
| 6.5 (77–79) | 6 | 6 | | 5 |
| 7.5 (89–92) | 8 | 8 | | 8 |
| 8.5 (101–104) | 10 | 10 | | 8 |
| 9.5 (113–114) | 3 | 3 | | 3 |
| 10.5 | | | | |
| 11.5 (138) | 1 | 1 | | 1 |
| 12.5 (150–156) | 2 | 2 | | 2 |
| 13.5 | | | | |
| 14.5 (173) | 1 | 1 | | 1 |
| 15.5 (185) | 2 | 2 | 1 | 1 |
| 16.5 | | | | |
| 17.5 | | | | |
| 18.5 | | | | |
| 19.5 | | | | |
| 20.5 | | | | |
| 21.5 (260) | 1 | | | |
| *total* | *226* | *163* | *42* | *104* |

*Fig. 1. The number of known-age elk in the total sample, and the number of both sexes, males, and females in each age cohort with measurable m1 crown heights. Sex was not known for some specimens.*

## Measuring Tooth Crown Height

Following Klein and Cruz-Uribe (1984, 46–47), crown height was measured on all specimens as the minimum distance between the occlusal surface and the line separating the enamel of the crown and the dentine of the root (enamel-dentine junction) on the buccal-most surface of the anterior lobe of the tooth. Some researchers measure tooth crown height as the distance from the enamel-dentine junction to the "saddle" between the protoconid and hypoconid peaks on the buccal surface of a mandibular tooth (e.g. Gifford-Gonzalez 1991; Lowe 1967; Spinage 1971). This often is done when the cusps are damaged and cannot be measured (Gifford-Gonzalez 1991; Lowe 1967). Unfortunately, this "saddle" measurement may be biased, because it is not affected by wear until the peaks of the cusps of the tooth are worn. By not recording the early wear on the tooth, individuals might be recorded as younger than their actual age. Other researchers measure crown height on the lingual side of a mandibular tooth as the minimum distance between the occlusal surface (the metaconid or entoconid peaks) and the enamel-dentine junction (e.g. Koike and Ohtaishi 1985; Lister 1981). I expect that lingual crown height measurements have a comparable relationship with age as buccal crown height measurements, because metaconid height is highly correlated to protoconid height, i.e. n = 47, $r$ = 0.97 (Steele 2002). The lingual surface of a mandibular tooth is fairly flat so the lingual measurement is harder to define consistently than the buccal measurement, particularly once the cusps have worn flat. Also, the lingual measurement is awkward to take on comparative material when the hemi-mandibles are still articulated. The crown height measurement described by Klein and Cruz-Uribe (1984, 46–47) is preferable to the other measurements, because it is easy to define (i.e. has a low inter-observer measurement error), easy to take, and has become standard practice in zooarchaeology (e.g. Gaudzinski 1995; Hoffecker, Baryshnikov, and Potapova 1991; Morrison and Whitridge 1997; Pike-Tay 1991; Pike-Tay, Morcomb, and O'Farrell 2000; Slott-Moller 1990; Walker 2000).

Measurements were taken on dp4, p4, m1, m2, and m3. The right mandible was measured unless it was missing or damaged (lefts measured: n = 14), and pathological specimens were omitted. In this initial investigation into the relationship between crown height and age, I analyzed only the measurements on m1,

because this tooth had the largest sample size (Fig. 1, n = 163). The first molar could not be measured on the youngest individuals, because the tooth had not yet erupted enough to expose the enamel-dentine junction, nor on the oldest individual (260 months), because the crown was completely worn away and only roots remained.

One difficulty with using m1 to estimate age-at-death in fossil specimens is that in many ungulate species, it can be difficult to separate isolated m1s from m2s, as they are morphologically similar. Klein *et al.* (1981) addressed this problem in their initial investigation into the utility of mathematical equations to estimate age-at-death from tooth crown heights in *C. elaphus*. They found that length and particularly breadth measurements clearly separated m1s from m2s with minimal overlap, supporting the visual impression that m2s are more massive than m1s. These results were similar whether the teeth were isolated or in mandibles. Investigations into my own fossil and modern data confirm these results. Because the size difference is relative, measurements will not help identify m1s versus m2s when only a few teeth are present, but small samples cannot provide meaningful mortality profiles regardless. Thus, isolated teeth from an archaeological sample can be visually compared and measured to separate m1s from m2s when samples are large enough to create mortality profiles. An alternative is to use m3s to create mortality profiles, because they are more readily identifiable due to their third lobe. However, to make a complete mortality profile, deciduous teeth (often dp4) need to be considered in conjunction with adult teeth. Although m3 erupts at about the same time dp4 is shed (Brown and Chapman 1991; Lowe 1967; Quimby and Gaab 1957), m3 crown height is not measurable until well after the dp4 is shed, because the enamel-dentine junction is not visible until approximately 54 months (Steele, personal observation). Because of this, there would be a gap from approximately 26 months to 54 months in a mortality profile created from the combination of dp4 and m3. However, m3 can be used to examine age distributions in older individuals.

Tooth wear rates may vary between individuals and populations, possibly because of differences in diet (Flook 1970; Hewison *et al.* 1999; Skogland 1988) or degree of enamel mineralization (Kierdorf and Becher 1997). However, as Spinage (1973) suggested, teeth are critical for survival; it would be surprising if they varied widely in efficiency in a single species, because animals acquire energy by using their teeth to eat. Lowe (1967) found that teeth of *C. elaphus* from German forests had similar wear per age patterns as *C. elaphus* from Rhum, Scotland, although the climate, habitat, and management were very different. Any method of assessing age from wear on teeth, either by coding stages or measuring crown heights, assumes that individual and between population variation in timing of eruption and rate of wear is limited. They assume that individual variation is random, and the method must not consistently over- or under-estimate the ages of animals (Spinage 1973). Because of potential for variation, age-at-death estimates based on wear cannot accurately assign age to narrow ages classes, however, this study investigates their utility in assigning specimens to broader age classes, such as 10% of life span.

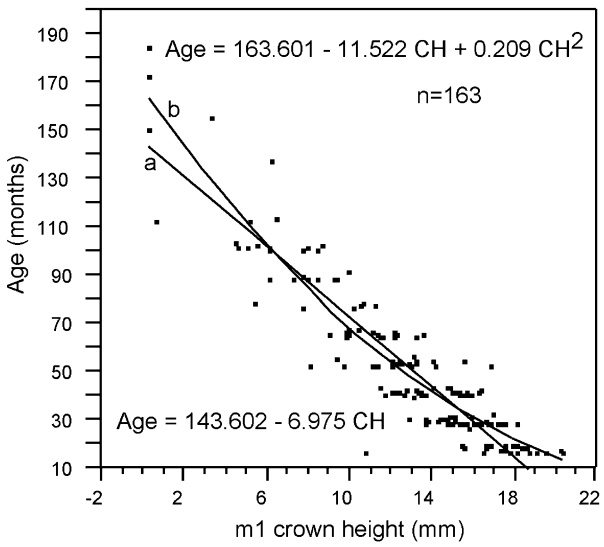


*Fig. 2. Linear (a) and quadratic (b) regressions of age on crown height for the known-age sample of elk. Summary statistics are provided in Fig. 3.*

## The Relationship Between Crown Height and Age

In order to determine the nature of the relationship between crown height and age, I performed both linear and quadratic regressions of age in months on tooth crown height for m1 (Fig. 2). There is discussion in the literature about whether inverse or classical calibration should be used to estimate an unobservable quantity (e.g. age-at-death, stature) from observable dental or skeletal measurements (Aykroyd *et al.* 1999; Aykroyd *et al.* 1997; Dapson 1980; Konigsberg *et al.* 1998). As the purpose of this study is to adjust the theoretical equation used in the QCHM and not direct predictions from the regression equation, I chose to use inverse calibration because it produces a quadratic equation that is directly comparable to the QCHM equation.

The quadratic regression provides a slightly better fit to the data than the linear regression (Fig. 3). Pike-Tay *et al.* (2000) also found that quadratic regression lines better fit their large sample (n = 999) of known-age barren-ground caribou (*Rangifer tarandus*, Linnaeus 1758). In Morrison and Whitridge's (1997) study of known-age barren-ground caribou from the same

| *sample information* | *m1* |
|---|---|
| sample size (n) | 163 |
| mean age (months) | 53.5 |
| standard deviation of age (months) | 33.1 |
| mean crown height (mm) | 12.9 |
| standard deviation of crown height (mm) | 4.3 |
| *linear regression* | |
| coefficient of determination ($r^2$) | 0.84 |
| standard error of estimate (months) | 13.26 |
| y-intercept | 163.6 |
| *quadratic regression* | |
| coefficient of determination ($r^2$) | 0.87 |
| standard error of estimate (months) | 12.09 |
| y-intercept | 143.6 |

*Fig. 3. Summary of regressions of age on crown height.*

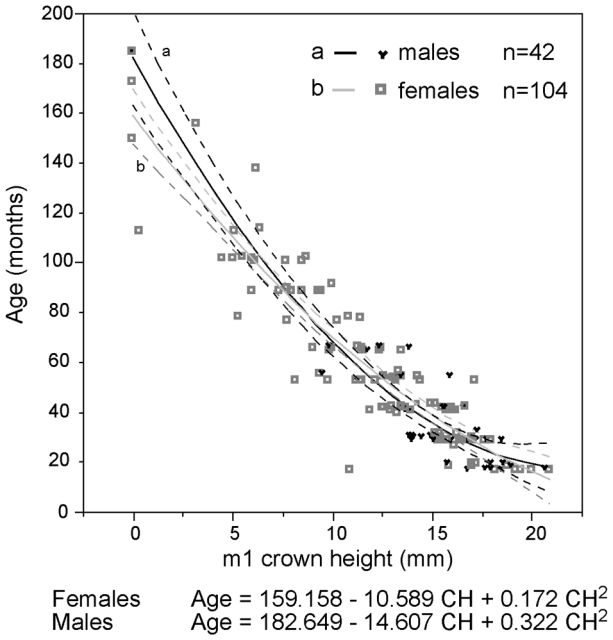


*Fig. 4. When quadratic regression equations are calculated for males (a) and females (b) of known-age elk separately, the confident intervals around the two regression lines overlap, indicating that differences in wear rates between males and females cannot be detected.*

population as Pike-Tay *et al.*'s (2000) sample, they found that linear equations adequately predicted age, but this discrepancy is possibly due to smaller sample size (n = 78). However, Morrison and Whitridge (1997) suggest that the quadratic equation may be "overly precise" for semi-hypsodont caribou, and therefore, the linear equation is sufficient. These results support Spinage's (1971) proposal that teeth will start wearing rapidly, but then the wear rate will decelerate as the occlusal surfaces become smooth. The magnitude of the standard error suggests that it should be possible to estimate age-at-death within approximately ± 1 year. Klein *et al.* (1983) had similar results in their study of the original known-age elk sample.

## Assessing Differences in Toothwear Between Males and Females

One potential source of error when estimating age-at-death from tooth wear is a different wear rate between males and females. I investigated this by regressing m1 crown height on age as in Fig. 2, but I calculated separate regression lines for males (n = 42) and females (n = 104; Fig. 4). When 95% confidence intervals are defined for each line, they overlap for their entire length. This indicates that differences in wear rates between males and females cannot be detected in this sample. This is fortunate because sex usually cannot be identified in fossil *C. elaphus* dental remains.

The lack of differences between the sexes in this sample of elk is supported by studies of caribou and white-tailed deer (*Odocoileus virginianus*, Zimmermann 1780). In Pike-Tay *et al.*'s (2000) large sample of known-age caribou, they found no differences in wear rates between the sexes. In contrast, when Morrison and Whitridge (1997) regressed age on m1 crown height for their sample of caribou, they obtained different linear regression lines for the sexes, although they did not provide statistical results. By examining the data they provided in an Appendix to their paper, I was able to determine that the slopes of the male and female regressions lines are different and this difference in wear rates holds even when the confidence intervals around the lines are considered. It is unclear why Pike-Tay (2000) and Morrison and Whitridge's (1997) results differ. Van Deelen *et al.* (2000) studied white-tailed deer (n = 100) from Illinois, United States whose age-at-death had been assigned by counting cementum annuli. They measured crown height as the maximum height from the occlusal surface to the stains at the tooth gum line, and they found no differences in degree of wear between m1s of males and females.

## Estimating Age-at-Death

I assessed the ability of the regression equations to predict age-at-death by plotting residual values against known ages for the known-age sample of elk (Fig. 5). I calculated the residuals by subtracting the age assigned by the regression equation from the known age for each specimen. A residual of '0' is a perfect estimation, while a positive value shows that age has been underestimated and a negative value shows that age has been overestimated. In Fig. 5, the width of the correct 10% of life span age class (19.2 months and centered on residual = 0) is darkly shaded and the adjacent two 10% of life span

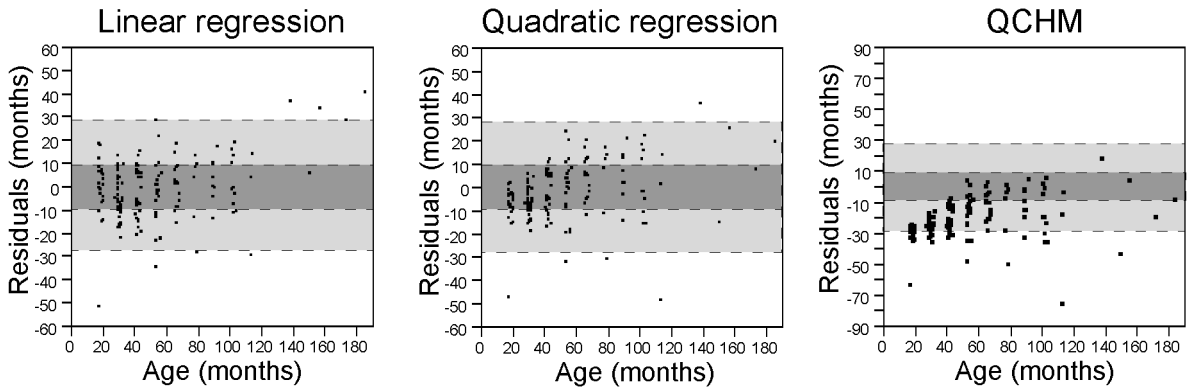


*Fig. 5. Known-age plotted against known-age minus the estimated age. Age was estimated using three equations: linear regression, quadratic regression, and the QCHM. Positive values are under-estimates and negative values are over-estimates. The darkly shaded regions approximate ±9.6 months (one 10% of life span age class), while the lightly shaded regions approximate the adjacent 10% of life span age class.*

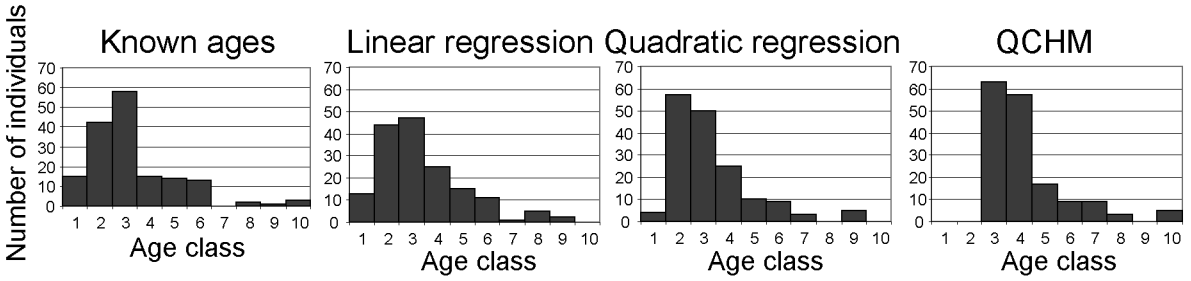


*Fig. 6. Histograms comparing the number of individuals in each age class using multiple methods of estimating age. The Kolmogorov-Smirnov test was used to see if the distributions created from the estimation techniques were similar to the known age distribution. The histograms of the linear and quadratic regressions were not significantly different from the known-age histogram, but the QCHM histogram was.*

ages classes are lightly shaded. This allows assessment of how well the regression equations estimate age. While there is a large amount of variation present at each age, age is almost always assigned to either the correct age class or to an adjacent one, as is suggested by the standard error of estimates. I created histograms of 10% of life span age classes using the age estimates from the linear and quadratic equations and compared them to a histogram of the known-age specimens (Fig. 6). Neither histogram based on age estimates was statistically different from the known-age histogram using the Kolmogorov-Smirnov test (linear: K = 0.61, p = 0.95; quadratic: K = 0.61, p = 0.95).

The regression equations appear to adequately estimate age from crown height in this sample of known-age Rocky Mountain elk. If age estimates were needed only for elk with the same sized teeth, then the regression equations are sufficient. However, faunal analysts need to assign ages in a variety of populations whose teeth and life histories may have different parameters. This is especially true for *C. elaphus* whose body and tooth size vary across space and through time. The regression equations are only suitable for populations with teeth the size of Rocky Mountain elk, one of the largest subspecies of elk (Geist 1998, 349–350). Enloe and Turner's (in this volume) study of reindeer (*R. tarandus*) confirmed that initial unworn crown heights need to be population specific and therefore that general regression equations are not adequate for estimating age-at-death in species whose tooth size varies. Because of this variation, it is desirable to have a theoretical formula in which initial crown heights and other values can be sample specific.

## The Quadratic Crown Height Method

Spinage (1971) first proposed a wear model for using crown heights to estimate age-at-death of hypsodont ungulates. It has been tested with known-age samples of Rocky Mountain elk by Klein and colleagues (Klein,

Allwarden, and Wolf 1983; Klein and Cruz-Uribe 1983; Klein *et al.* 1981), bison (*Bison bison*, Linnaeus 1758) by Gifford-Gonzalez (1991), and barren-ground caribou by Pike-Tay *et al.* (2000). The technique, now known as the Quadratic Crown Height Method (QCHM), employs a set of quadratic formulae based on a variable rate of wear that can be used to predict age-at-death from tooth crown height when the unworn tooth crown height and the age when tooth crown height reaches '0' are known. Unlike the eruption and wear methods, the QCHM is easy to replicate, is objective, and can be utilized with isolated teeth.

Spinage's model (1971; 1972; 1973) is based on the observation that when crown height is plotted against age, wear rate is not linear but actually slows with age. This may be because the opposing occlusal surfaces m1 become smoother, and friction thus decreases, and as m2 and m3 begin to wear, friction on anterior surfaces further decreases (Spinage 1971). The QCHM assumes that when the permanent teeth are worn completely away (crown height equals '0'), the animal dies. Ideally the age when crown height equals '0' would be calculated for each tooth from large known-age samples, but these data are unavailable for most species. Instead, the age of potential ecological longevity must be used as an approximation. Potential ecological longevity is not the mean life span for the species, but the maximum age that a wild individual can reasonably obtain.

The QCHM formulae are (from Klein, Allwarden, and Wolf 1983, 49):

For deciduous teeth: $AGE = AGEs\ [(CH\text{-}CH_0)/CH_0]^2$

For permanent teeth: $AGE = (AGEpel\text{-}AGEe)\ [(CH\text{-}CH_0)/CH_0]^2 + AGEe$

Equations are calculated by substituting the appropriate values for each tooth. AGEs is the age at which the deciduous tooth is shed, AGEe is the age at which the permanent tooth erupts, and AGEpel is the potential ecological longevity of individuals of the species. $CH_0$ is the mean initial unworn crown height for each tooth type for the sample under study, and CH is the crown height of the specimen for which age is being assigned. Ages are measured in months, and crown heights are measured in millimeters.

The appropriate values for Rocky Mountain elk can be obtained from wildlife biology. The potential ecological longevity for individuals of this population is 192 months (Houston 1982), and m1 erupts through the gum at 6 months (Quimby and Gaab 1957). These two variables appear to be consistent across subspecies (Brown and Chapman 1991; Lowe 1967; Lowe 1969), so they can be used for populations where these ages cannot be directly ascertained. Average unworn tooth crown height needs to be determined for each sample, and for Rocky Mountain elk the measurement is 27.0 mm (Klein and Cruz-Uribe 1984, 49). Tooth crown height is determined for each specimen. I used these values in the QCHM formula to estimate age-at-death from m1 crown height measurements on the known-age sample of elk.

I tested the ability of the QCHM to adequately estimate age-at-death by plotting the residuals and creating a histogram in the same manner as with the regression estimates. It is apparent that the QCHM overestimates the age-at-death of the specimens, and this bias occurs more frequently for younger individuals (Fig. 5). The histogram of the ages estimated with the QCHM is significantly different from the histogram of known-ages ($K = 3.16$; $p < 0.001$). As formulated, the QCHM did not satisfactorily estimate age-at-death.

## Adjustments to the QCHM

Because there is still a need for a flexible equation that can be used to estimate age-at-death in archaeological specimens, I examined the QCHM equation further to determine if it could be adjusted to provide more reliable estimates of age-at-death. Following Pike-Tay *et al.* (2000), I investigated two aspects of the equation: 1) AGEpel, the age of potential longevity, and 2) the degree of curvature of the line created by the equation.

One reason for discrepancies between the theoretical formulae and regression equations is that tooth crown height does not always equal '0' when an animal reaches the age of potential ecological longevity. For m1, teeth can be worn past the crown-root junction before the animal dies (Spinage 1972; Steele, personal observation). The known-age elk sample has one 150-month-old individual with an m1 crown height of '0'; all individuals 173 months and older ($n = 4$) have m1 crown heights of '0', and one 156-month-old individual still has a measurable crown height. In all of these cases, p4, m2, and m3 still have crown remaining. Only one 260-month-old individual has m2 and m3 crown heights of '0'; m1 is completely worn away, but p4 still has a measurable crown. Based on these data, AGEpel should be changed in the QCHM formulae to the age at which the crown height of each tooth type reaches '0', as suggested by Klein *et al.* (1983). This value can be considered the average age of the tooth's potential longevity (AGEtpl). At the moment, the known-age data set has too few older animals to obtain AGEtpl empirically, so I calculated the y-intercept values, i.e. the ages when crown height reaches '0', from the quadratic regressions. For m1, the y-intercept is 163.6 months.

I substituted AGEtpl (163.6 months) for AGEpel in the QCHM's formula for estimating age from m1 crown height. All other values stayed the same. The resulting equation is shown in Fig. 7, along with a plot of the residuals for the estimated ages. The adjusted formula estimates age within the correct 10% of life span age class for the majority of m1s, and all but a few are within

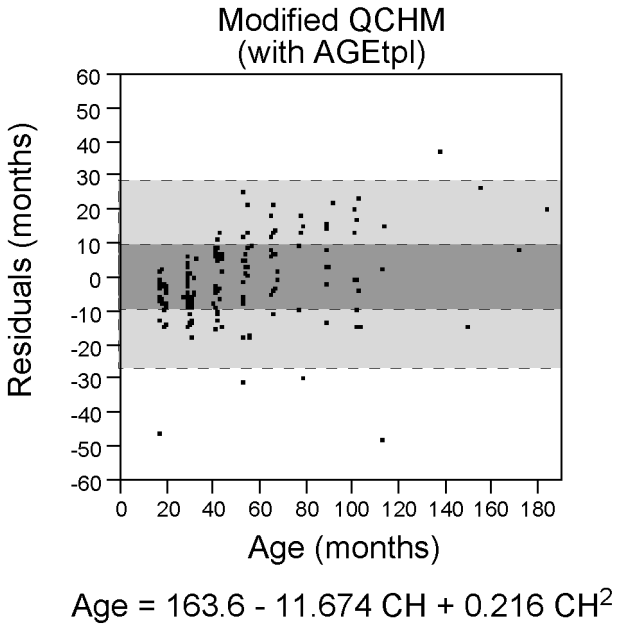


*Fig. 7. Known age plotted against known age minus the age estimated for m1s in the known-age elk sample. Age was estimated using a modified QCHM equation where AGEtpl, the y-intercept value of the regression equation, was substituted for AGEpel. The y-intercept value predicts the age at which m1 crown height will reach '0', here 163.6 months. The darkly shaded region approximates ±9.6 months (one 10% of life span age class), while the lightly shaded regions approximate the adjacent 10% of life span age classes (life span is still considered to equal AGEpel or 192 months*

one adjacent age class; changing AGEpel to AGEtpl greatly increased the reliability of the theoretical formula. Importantly, the histogram constructed with the new theoretical formula is not statistically different from the histogram of the known-age individuals (K = 0.56; p = 0.999; Fig. 8).

Klein *et al.* (1983) also argued that AGEpel needed to be adjusted in the QCHM to equal the age when crown height reaches '0', but they decided that their known-age sample size was too small to accurately adjust the formula. They had to assume that when tooth crown height equals '0', the animal dies, and therefore the maximum age reached by wild individuals would approximate the age at which tooth crown height equals '0' for any tooth (see also Spinage 1973). The increased sample size presented here allows for more confidence in the adjustments. The more accurate predictions – granted that the predictions are on specimens that provided the adjustment – seem to justify changes to the AGEpel. In their study of known-age caribou, Pike-Tay *et al.* (2000) changed AGEpel to AGEmax, the average maximum life span, which they use for all teeth. This value is the same age in months as the potential ecological longevity, but they were trying to clarify what that variable represented.

Adjusting the value of animal potential longevity to tooth longevity presents an additional problem for m1. The age of tooth longevity (163.6 months) is lower than the age of animal longevity (192 months), so when estimating age from m1, no specimens will ever be assigned an age above 163.6 months. This means that when creating mortality profiles based on 10% of life span, no m1 specimens will be placed in Age Class 10. If this bias is consistent across all samples, it should not interfere with interpretations of the data.

I also investigated if a quadratic equation provides the most accurate description of the relationship between crown height and age; it is possible that a line with a different shape may better fit the data. By modelling the QCHM equation as the allometric growth curve, it is possible to empirically determine the best exponent for the equation (Steele 2002). The allometric growth equation has been used successfully to model many biological relationships, so it is logical to apply it to toothwear. When I did this for the known-age elk sample, the resulting exponent was 1.99 (95% confidence interval of 1.84–2.14). The exponent of 2 in the QCHM, as traditionally formulated, is right in the middle of the confidence interval. This confirms that a quadratic equation is appropriate for m1.

## Comparisons with Other Cervids

I compared the m1 wear rates of three species of cervids: the elk sample studied here (Klein, Allwarden, and Wolf 1983; Klein and Cruz-Uribe 1983; Klein *et al.* 1981; Steele 2002), barren-ground caribou (Morrison and Whitridge 1997), and white-tailed deer (unpublished data collected by C. Wolf). Visual comparisons of these three species supports species-specific adjustments to the QCHM formulae (Fig. 9). Caribou m1s wear more slowly than elk m1s, because caribou have lower crowned teeth than elk but the two species have similar maximum life spans. In their adjustment of the QCHM for caribou, Pike-Tay *et al.* (2000) changed the degree of curvature to reflect this. They found that an exponent of 1.6 provided a better fit to the data than an exponent of two. Caribou and white-tailed deer have similar initial unworn crown heights, but it appears that white-tailed deer teeth initially wear more rapidly than caribou teeth. Further investigation into the white-tailed deer sample will allow the parameters of the QCHM equation to be adjusted to this species.

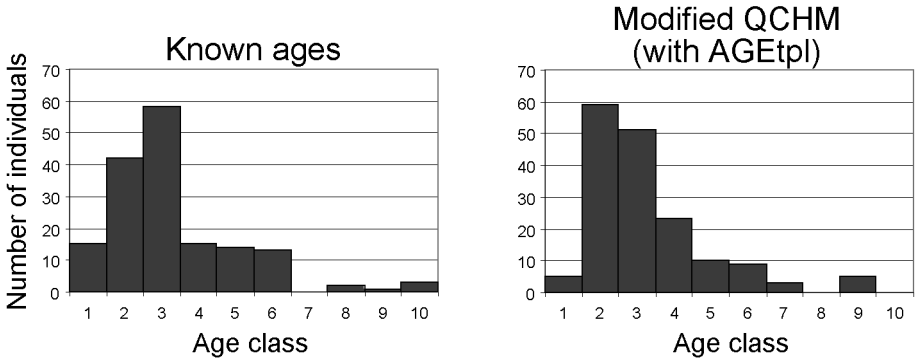


*Fig. 8. Histograms comparing the known-age distribution to the distribution of individuals in each age class using the modified QCHM equation for m1. When age classes are calculated using AGEtpl, the histogram does not differ significantly from the histogram based on known ages.*

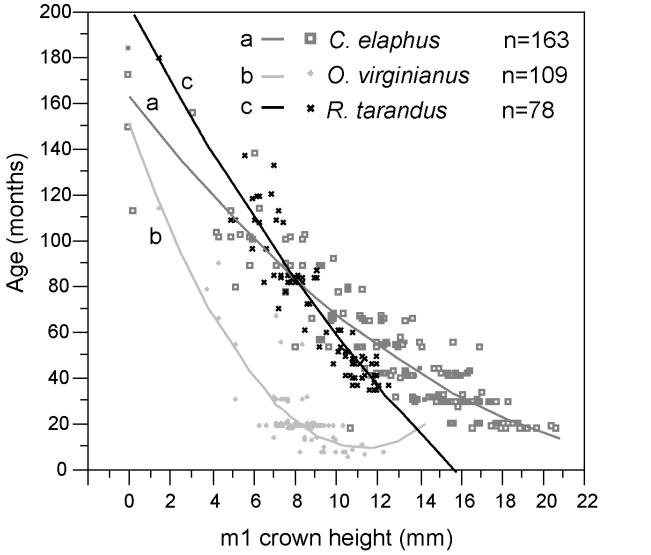


*Fig. 9. Quadratic regressions of age in months on m1 crown height for three species:* C. elaphus *(a; Klein, Allwarden, and Wolf 1983; Klein and Cruz-Uribe 1983; Klein* et al. *1981),* O. virginianus *(b; unpublished data collected by C. Wolf), and* R. tarandus *(c; Morrison and Whitridge 1997, 1105–6).*

## Conclusions

Tooth crown heights provide an objective and replicable way to assess the degree of wear on a tooth. They can be used to estimate age class, but not narrow age estimates. For accurate age-at-death estimations for species whose size changes through time and across space, population-specific parameters need to be used instead of a generic species-specific regression equation. This can be done with the QCHM, where unworn tooth crown height for each population can be substituted into the equations. However, the appropriateness of the equation for each species under consideration should be investigated using known-age specimens of that species, because as originally formulated, the QCHM did not predict satisfactorily age-at-death for a known-age sample of *C. elaphus*. Using large known-age samples, it is possible to adjust the equations to fit species-specific parameters. The adjusted equations can be applied to archaeological samples with the assumption that what we know about modern animals will also be true of prehistoric animals. Adjustments such as those discussed here are not feasible for extinct species, but parameters from closely related species might be adequate. For more accurate estimations, the age of potential ecological longevity (AGEpel) should be changed to the average age of the tooth's potential longevity (AGEtpl). AGEtpl needs to be empirically determined for each tooth type for each species using known-age samples. For the known-age elk sample, I estimated AGEtpl from the y-intercept of the quadratic regression of crown height on age. Using the adjusted equation, age class is more accurately estimated from tooth crown heights. In addition, using the known-age sample, I was able to confirm that a quadratic equation can be used to describe the relationship between m1 and age.

*Acknowledgements*
This research was first described in my Ph.D. thesis, and R. Klein, E. Hadly, and J. Rick commented on it in that context. R. Carden and R. Carter gave helpful suggestions for improving this manuscript, while J. Enloe and A. Pike-Tay provided fruitful discussions. T. Weaver assisted in all stages of the project. R. Klein generously shared C.

Wolf's data. K. Hamlin (Montana Fish, Wildlife, and Parks-Bozeman), L. Irby (Montana State University-Bozeman), and D. Dyer (University of Montana) provided access to known-age material. The L.S.B. Leakey Foundation, Andrew W. Mellon Foundation, and Department of Anthropological Sciences, Stanford University funded this research. This paper was presented as part of the Ageing and Sexing session organized by Deborah Ruscillo at the ICAZ meetings in Durham, England, August 23–28, 2002; thank you for allowing me to be part of this wonderful symposium and for your great organizational skills. I would also like to acknowledge the generous travel grant from the Institute for Aegean Prehistory which allowed me to attend the meeting.

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*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 129–144*

# 8. Methodological Problems and Biases in Age Determinations: a View from the Magdalenian

*J. G. Enloe and E. Turner*

*Numerous methods and procedures have been proposed for the construction and interpretation of age and mortality profiles of archaeological faunal assemblages. Variations in the results and biases in the methods have great implications for the interpretation of selective strategies for hunting or for culling of domesticated herds. Taphonomic factors often bias faunal assemblages against the recognition of the youngest cohorts of archaeological populations. Paradoxically, it appears that some methods based on use wear measurements bias results in the opposite direction, either collapsing age categories of the oldest individuals or enhancing out of proportion the counts of the youngest adult individuals. This paper explores methodological considerations of dentally based age determinations. It focuses on various methods of crown height measurements, particularly comparing profiles derived from single tooth measurements with those from averaged tooth row or reconstructed individuals' dental series. Data including observations on reindeer and horse dental material from the Magdalenian sites of Verberie and Solutré, France, are used to investigate potential variability in results and its implications for interpretations of hunting strategies in the Paleolithic. These dental studies indicate that mortality profiles determined from measurements of single teeth may yield misleading results in the proportions of adults and juveniles. Further, scenarios of exclusively prime-age prey selection by technologically superior Upper Paleolithic hunters may need to be re-evaluated.*

## Introduction

Numerous methods and procedures have been proposed for the construction and of age and mortality profiles of archaeological faunal assemblages. Variations in the results and biases in the methods have great implications for the interpretation of selective strategies for hunting or for culling of domesticated herds (Kurtén 1953; Voorhies 1969; Klein 1982, Stiner 1990). Taphonomic factors often bias faunal assemblages against the recognition of the youngest cohorts of archaeological populations. Paradoxically, it appears that some methods based on use wear measurements bias results in the opposite direction, either collapsing age categories of the oldest individuals or enhancing out of proportion the counts of the youngest adult individuals. This paper explores methodological considerations of dentally based age determinations. It focuses on various methods of wear stages and crown height measurements, particularly comparing profiles derived from single tooth measurements with those from averaged tooth row or reconstructed dental series of individuals. Data including observations on reindeer (*Rangifer tarandus*) and horse (*Equus* sp.), and dental material from the Magdalenian sites of Verberie and Solutré, France, are used to investigate potential variability in results and its implications for interpretations of hunting strategies in the Paleolithic.

## Age Determinations at Verberie: Reindeer and Quadratic Equations

Analytical results re-evaluating ages of the reindeer remains from Verberie (Audouze *et al.* 1981; Audouze

1987; Audouze and Enloe 1997), presented at the 2001 Society for American Archaeology meetings (Enloe 2001), indicated that age determinations were substantially different from previous results (c.f., Enloe 1997). This has led to the reconsideration of the methodological underpinnings of the creation of mortality profiles. A variety of methods have been used to derive age class information, including most notably wear stages and crown height measurements. While the latter technique has generally come to be seen as more accurate, a number of methodological issues have arisen as more data sets are examined. This analysis compares several techniques for age calculation from crown height measurements, using data from the mandibular dental remains from six occupation levels at Verberie. Many of the mandibles were subjected to refitting, completing the tooth rows from loose individual teeth, and matching the left and right tooth rows with their bilaterally symmetrical pair from the opposite side. A total of 128 individuals were identified, with tooth counts ranging from one to ten for each individual. The refitting was intended to shift the age determination to a focus on individual animals, rather than on individual teeth.

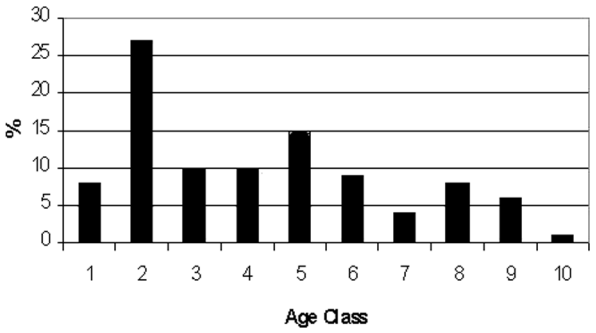


*Fig. 1. Mortality profile of age classes based on Bouchud's (1966) tooth wear stages for the Verberie reindeer population.*

### *Wear stages*

Initial inspection used Bouchud's (1966) wear stages, with results expressed in age classes of 10% of lifespan (Fig. 1). This yielded a mortality profile with two interesting features. First was a peak in the second age class and a relatively weak showing of the first age class. This is normal, in that juveniles make up a very large proportion of living populations, and that taphonomic factors may lead to under-representation of the smaller, more fragile first-year individuals. Second was a minor bulge in the fifth age class. This was interpreted as corresponding to selection for prime-age individuals, which Stiner (1990) has suggested as the hallmark of modern human hunting practices.

### *Crown heights*

Despite the fact that they are based on examination of individual mandibles rather than individual teeth, Bouchud's wear stages have often been criticized (e.g. Spiess 1979, 70–75). There is too much variation in the eruption schedule of permanent molars and premolars, and significant differences in rates of wear of different individuals (Miller 1974; Skoog 1968). Perhaps more significant are the problems of inter-observer error and isolated teeth (Steele 2002, 2006 this volume). An alternative method is offered by crown height measurements (Lowe 1967; Spinage 1971, 1972, 1976; Klein *et al.* 1983; Klein *et al.* 1981; Levine 1982, 1983), which may avoid some of the subjective classification of wear stages. Spinage (1971) noted that tooth wear is not linear, occurring faster on the smaller surface area of high crowns than on the increased surface area of worn teeth. To account for this, Klein *et al.* (1983) proposed the application of a quadratic equation to crown height measurements of *Cervus elaphus* to estimate age-at-death of individuals.

Gifford-Gonzalez (1991) assessed crown height measurements and formula for age determination from Klein *et al.* (1983) against two known-age samples of bison (*Bison bison*). She found serious problems in the application. She noted directional bias in age estimates derived from their formulae in particular, resulting in overestimation of young individuals. She credited this to a molar sparing effect, in which bison molars wear much more slowly during their first few years than is predicted by the quadratic equation. She concluded that some of the differences in results of her and the Klein *et al.* (1983) study might be due to the different species being studied. This finding suggests that "better results in using remnant crown heights to age ungulates can probably be obtained by deriving predictive equations from studies of known-age species, preferably conspecifics of the archaeological or paleontological taxon under study" (1991, 76).

It was in this vein that Pike-Tay *et al.* (2000) tested the quadratic regressions of age on a large, known age sample of the Kaminuriak herd of *Rangifer*, and then modified the equations, to achieve a better fit to the curve of the known-age population. The formula for each premolar and molar is presented in Fig. 2. This provided the perfect control sample to apply the method to the same species in a prehistoric population at Verberie.

The equations for third and fourth premolars and for first, second and third molars were used as a basis for age calculations for each permanent tooth. Lowe (1967) has suggested that individuals of the same age exhibit substantial variation in crown heights of the same tooth, although his height measurements were taken at the saddle between cusps rather than at the highest point of

$P_3$ Age=200–(2(200–24) (CH/12.433))+((200–24) ($CH^{1.5}$) /($12.433^{1.5}$)) + (((12.433-CH)$^2$)/1.25)
$P_4$ Age=200–(2(200–24)(CH/13.811))+((200–24) ($CH^{1.5}$) /($13.811^{1.5}$)) + (((13.811-CH)$^2$)/1.25)
$M_1$ Age=200–(2(200–5)(CH/ 15.490))+((200–5) ($CH^{1.6}$)/($15.490^{1.6}$))+ (((15.490-CH)$^2$)/3)
$M_2$ Age=200–(2(200–12.5)(CH/ 16.727))+((200–12.5) ($CH^{1.6}$)/($16.727^{1.6}$)) + (((16.727-CH)$^2$)/3)
$M_3$ Age=200–(2(200–24)(CH/ 14.990))+((200–24) ($CH^{1.6}$)/($14.990^{1.6}$)) + (((14.990-CH)$^2$)/3)

*Fig. 2. Pike-Tay* et al. *(2000) crown height age calculation formulae; crown heights are in mm and age calculation yields months.*

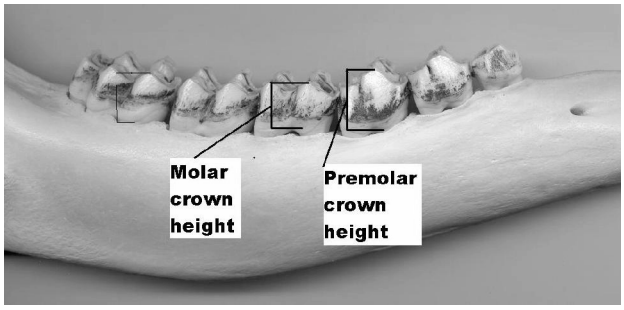


*Fig. 3. Measurement locations for buccal crown height measurements on premolars and molars of reindeer.*

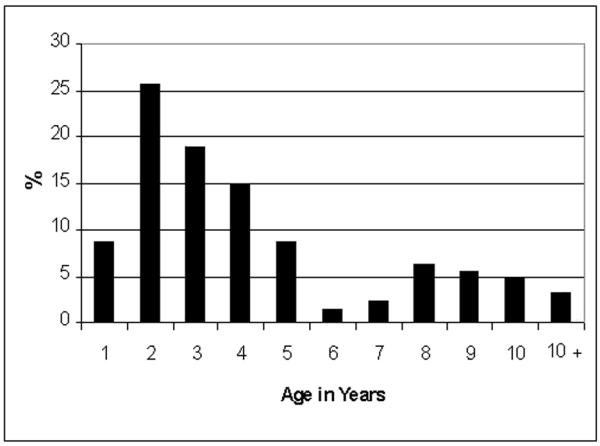


*Fig. 4. Proportions of age classes of Verberie* Rangifer *population, calculated by averaging Pike-Tay (2000) tooth equations for each individual (from Enloe 2001).*

the anterior cusp, as was the case in this study (Fig. 3). The thrust of this analysis is that grouping of the teeth into identifiable individuals should allow us to estimate age based on the mean age of teeth for each individual despite variation in eruption scheduling among the different teeth. Therefore, all of the individual tooth calculations were averaged for each individual animal. Unfortunately, not every identified individual consisted of complete left and right mandibular tooth rows, so variation in the reliability of contribution of each tooth to the averaged age is difficult to calculate. Pike-Tay *et al.* (2000) suggested that problems in extreme height variability in youngest age classes necessitate calculation of their age by other means, so deciduous wear and permanent eruption stages were used to place individuals in the first three age classes. The individual-averaged age calculations yielded reasonably similar mortality curves for the occupation surfaces at Verberie, each characterized by substantial proportions of individuals in the second and third year cohorts (Fig. 4). This allowed construction of an argument for selection of pre-reproductive subadults and young adults, rather than prime-age individuals, as previously suggested by the wear stage analysis (Enloe 2001).

Further examination of this assemblage began to reveal problems with these first crown height analyses. The initial crown height figures for unworn teeth, which are the basis for the quadratic equations, did not correspond very well to the Verberie assemblage, which were substantially taller in their initial, unworn state than were those of the Kaminuriak herd. If the teeth start out taller, they will always appear younger if age estimations are based on height measurements.

There were very few unworn teeth in the Verberie faunal assemblage from which to derive original crown

| Tooth | Kaminuriak herd (mm) | Verberie (mm) |
|---|---|---|
| $P_3$ | 12.433 | 19.49 |
| $P_4$ | 13.811 | 20.67 |
| $M_1$ | 15.490 | 18.76 |
| $M_2$ | 16.727 | 18.89 |
| $M_3$ | 14.990 | 18.11 |

*Fig. 5. Unworn crown heights for* Rangifer *mandibular cheek teeth, comparing Pike-Tay* et al. *(2000) values from the Kaminuriak caribou herd with those for the reindeer from the Verberie faunal assemblage.*

$P_3$ Age=200–(2(200–24)(CH/19.49))+((200–24)($CH^{1.5}$)/($19.49^{1.5}$))+(((19.49-CH)$^2$)/1.25

$P_4$ Age=200–(2(200–24)(CH/20.67))+((200–24)($CH^{1.5}$)/($20.67^{1.5}$))+(((20.67-CH)$^2$)/1.25)

$M_1$ Age=200–(2(200–5)(CH/18.76))+((200–5)($CH^{1.6}$)/($18.76^{1.6}$))+(((18.76-CH)$^2$)/3)

$M_2$ Age=200–(2(200–12.5)(CH/18.89))+((200–12.5)($CH^{1.6}$)/($18.89^{1.6}$))+(((18.89-CH)$^2$)/3)

$M_3$ Age=200–(2(200–24)(CH/18.11))+((200–24)($CH^{1.6}$)/($18.11^{1.6}$))+(((18.11-CH)$^2$)/3)

*Fig. 6. Revised crown height equations for Verberie. Crown heights are in mm and age is in months.*

height measurements. Some of the best examples were not completely erupted and were difficult or impossible to measure without destroying the mandibular ramus, which were being curated for other analyses. Crown height measurements for $P_3$ ranged from 2.67 mm to 19.49 mm. No unworn $P_3$ specimens were found or measured. Crown height measurements for $P_4$ ranged from 0.01 mm to 20.67 mm. Of the six $P_4$ specimens noted as being unworn, only five could be measured; they ranged from 12.80 mm to 18.55 mm. Crown height measurements for $M_1$ ranged from 3.26 mm to 18.76 mm; no unworn crowns could be measured. Crown height measurements for $M_2$ ranged from 4.69 mm to 18.89 mm; no unworn crowns could be measured. Crown height measurements for $M_3$ ranged from 6.22 mm to 18.11 mm. Four unworn specimens could be measured, ranging from 15.70 mm to 17.48 mm. In every case, the maximum crown height measurement for that tooth in the archaeological sample exceeded the maximum crown height measurement of notably unworn crowns. Clearly the range of original crown heights was greater than that of the small sample of unworn teeth. So the largest measurement obtained from the sample of specimens for each class of tooth was deemed to be original crown height (Fig. 5). The statistical variation within this very small sample would not be very meaningful, and this choice undoubtedly results in overestimation of age, but we simply do not have data for this prehistoric population that would be comparable to the thousand individuals in the Kaminuriak herd.

So the formulae were adjusted, substituting the taller measurements for each class of tooth, empirically derived from Verberie's own assemblage. The new formulae are presented in Fig. 6. With the new unworn crown height values, calculations were again run on all of the Verberie assemblage.

### *Individual tooth age estimations*

It should be noted immediately that very strong evidence for seasonality in the deciduous dentition of this faunal assemblage indicates a very narrow time frame for deaths making up the mortality profile. The evidence from Verberie suggests a fall migration interception kill of deer (Enloe 1997, 2001). The individuals in the first year cohort are approximately four months old; those in the second year cohort are approximately 16 months old. It follows that the third year and older cohorts have similar age categories. Therefore, age estimations in the first year should be very young, rather than at or near the 12 month boundary. It is thus very unlikely that, although $M_2$ could technically begin erupting as young as ten months, those teeth in this assemblage would belong to the first year cohort and they should therefore be placed in the second year cohort. This logic cannot, unfortunately, be carried over to the M3, since documented eruption could begin as early as 15 months or as late as 27 months; such teeth could belong to either second or third year cohorts. Most individuals probably fall into the third.

The revised age calculations can be compared to those of the original calculations on a tooth-by-tooth basis. The $M_1$ should have the highest sample size in most dental assemblages, as it is the first permanent tooth to erupt; this was the case for Verberie (n=115). Spiess (1979, 77) indicates eruption of $M_1$ between three and five months. Miller's (1974, 14) data indicate the absence of $M_1$ at one month, both erupting and teeth in occlusal position at five months, and only fully erupted teeth at ten months. Additional sampling observations between five and ten months might have been useful to give more information about variation in $M_1$ eruption. Spiess (1979, 77) suggests that no cheek teeth erupt during the first winter, providing a good punctuation in the eruption sequence. Pike-Tay *et al.* (2000) use 5 months as the eruption age for the $M_1$. The Pike-Tay calculation concentrates over 50% of the age determinations in the first five years, with the highest proportion in the second year (Fig. 7). A second mode occurs between 9 and 13 years. The revised calculation has virtually none in the first two years, with the largest proportion between three and ten years (Fig. 8). Another group of older individuals is represented from 12 to 17 years, with a maximum age at 19 years.

The sample size for $M_2$ in the Verberie population is almost as large (n=108). The $M_2$ calculations reveal a problem, as Pike-Tay *et al.* (2000) already noted, with almost 10% of the individuals' belonging to the first year cohort, while the mean eruption timing of this tooth might better be placed in the second year. Miller (1974, 14)

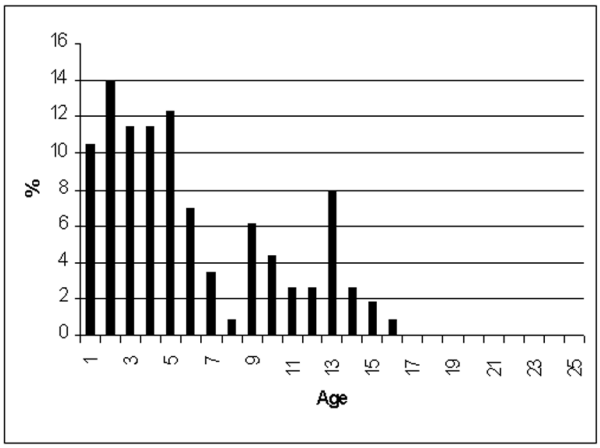


*Fig. 7. Results of first molar age classes derived from Pike-Tay* et al. *(2000).*

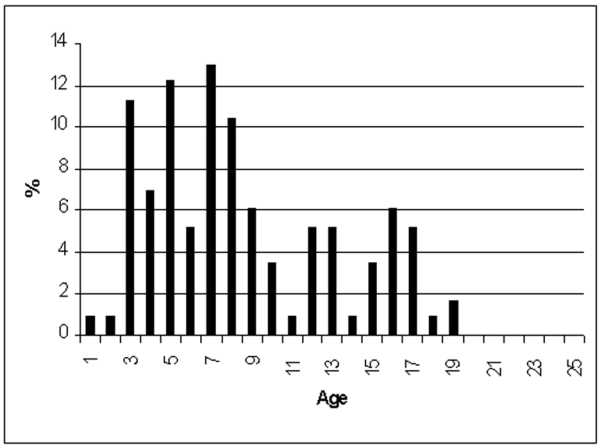


*Fig. 8. Results of first molar age classes derived from the revised formulae for Verberie crown heights.*

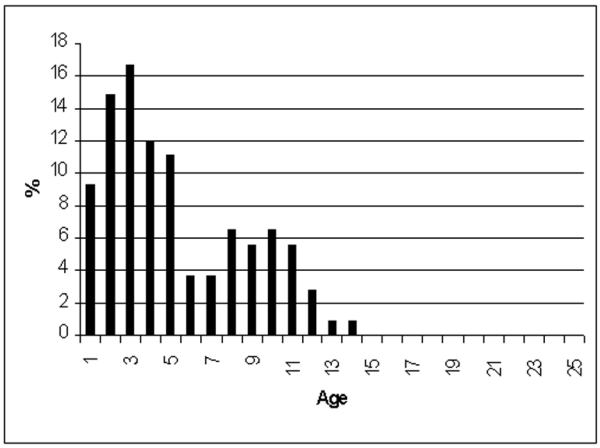


*Fig. 9. Results of second molar age classes derived from Pike-Tay* et al. *(2000).*

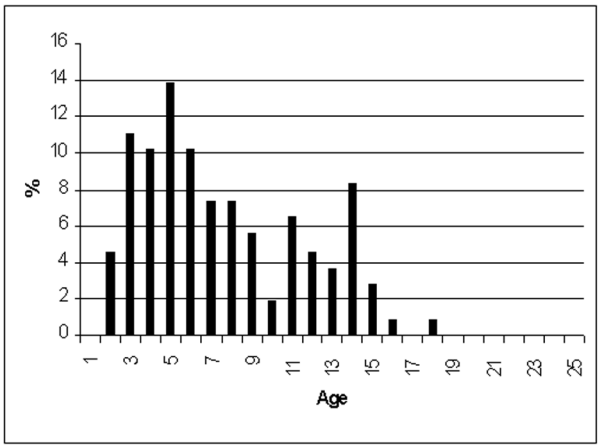


*Fig. 10. Results of second molar age classes derived from the revised formulae for Verberie crown heights.*

reports anomalous data on $M_2$ eruption from his samplings of the Kaminuriak caribou herd. At 10 months, 62% are absent, 38% are erupting and none are in permanent occlusal position. At 12 months 7% are absent, 77% erupting and 16% in occlusion. At 13 months, however, his sample included 40% absent, 33% erupting and 27% in occlusion. Spiess attributes this latter tardy state of eruption to sampling problems during one year, when a particular age cohort suffered from "late development due to bad weather or poor nutrition" (1979, 77). One might consider that the 12-month sample could be precocious and equally biased in the opposite direction by sampling problems. Pike-Tay *et al.* (2000) use 12 months as the eruption age for the $M_2$. Miller's (1974) data may be interpreted to suggest that an appropriate mean eruption age could be later than 12 months, rendering the Pike-Tay results too young. The Pike-Tay calculation (Fig. 9) is distinctly bimodal, with the strongest peak in the third year, and another from the eighth to twelfth. Ages range up to 14 years. The revised calculation (Fig. 10) shows no first year individuals, which is appropriate for the seasonality as discussed above; there is a peak in the fifth year and a decreasing number of individuals as age increases. There is a second peak at 14 years. Maximum age extends to 18 years.

Sample size for the third molar is smaller (n=81), as would be expected for the last erupting molar. Eruption of $M_3$ is more variable than that of the first two molars, ranging from 15 to 27 months. Miller's (1974) data show 92% and 65% absent at 15 and 17 months, and 61% and 94% in occlusion at 25 and 27 months. The anomalies previously mentioned in Miller's data for the $M_2$ are not apparent in the $M_3$ case, as absence percentage gradually decreases, erupting percentage increases and then de-

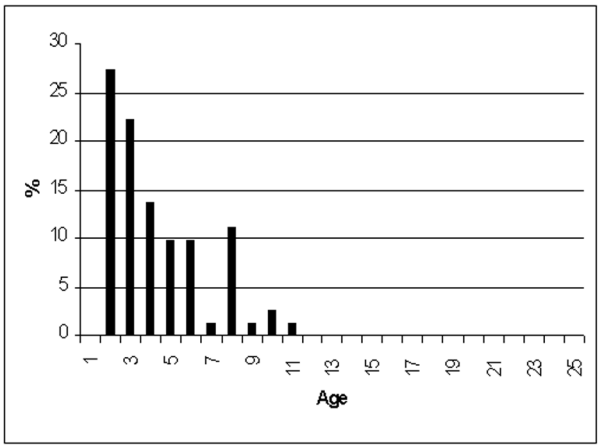


*Fig. 11. Results of third molar age classes derived from Pike-Tay* et al. *(2000).*

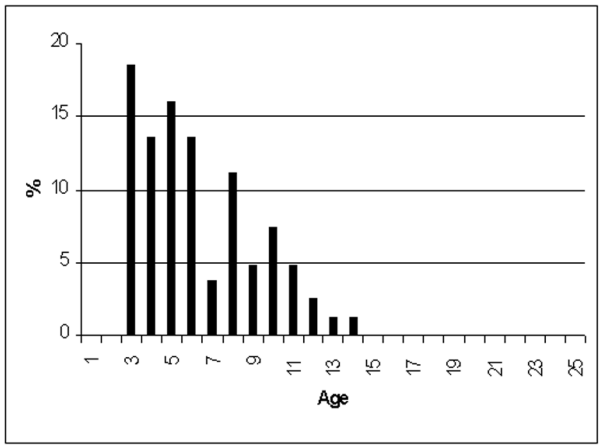


*Fig. 12. Results of third molar age classes derived from the revised formulae for Verberie crown heights.*

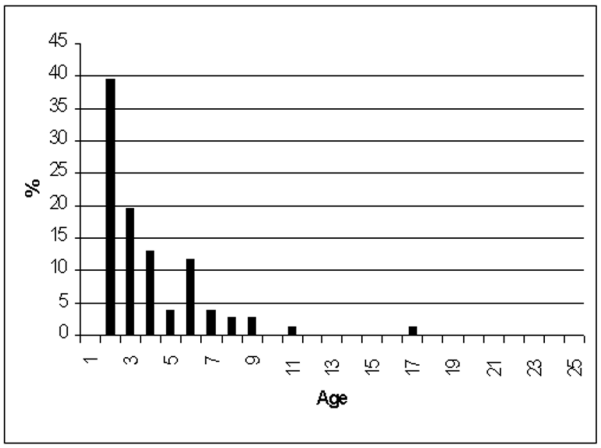


*Fig. 13. Results of third premolar age classes derived from Pike-Tay* et al. *(2000).*

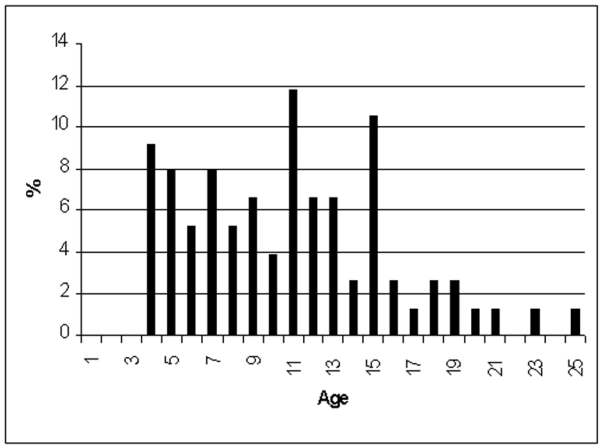


*Fig. 14. Results of third premolar age classes derived from the revised formulae for Verberie crown heights.*

creases, and permanent occlusal position percentage gradually increases from 17 to 29 months. Pike-Tay *et al.* (2000) use 24 months for the $M_3$ eruption date, at which point none are absent, half are erupting and half are in final position in Miller's sample. In this assemblage, one is trying to discern between 16 and 28month individuals. In the former, only about 20% of the third molars should be erupting, and none should be in occlusal position; in the latter, almost all should be in occlusal position. The $M_3$ calculations show the same contrast between the Pike-Tay calculation (Fig. 11) and the revised calculation (Fig. 12) as in the $M_2$. The Pike-Tay calculation assigns substantial numbers to the second year, where there should be very few erupted third molars; maximum age is 11 years. The revised calculation probably correctly assigns ages beginning with the third year and decreasing frequency with age up to 14 years.

Sample size for the third premolar is the smallest of the Verberie faunal assemblage (n=76). Miller (1974) documents erupting premolars from 22 to 27 months. While approximately half are in occlusal position by 24 months, 10% remain deciduous teeth through 27 months. All of Miller's sample were permanent teeth in occlusion by 29 months. While these data indicate that the $P_3$ should be erupting later than the $M_3$, Pike-Tay *et al.* (2000) use the same 24 months for the $P_3$ eruption date as for the $M_3$. The pattern seen in the $M_2$ and $M_3$ continues with the $P_3$, with an overwhelmingly young sample by the Pike-Tay formula (Fig. 13), including the highest proportion of individuals in the second year group, who should still have their deciduous dentition. Most individuals are under ten years, with only two outliers at 11 and 17 years. This is contrasted with the results of the revised formula (Fig. 14) indicating a more even distribution with decreasing

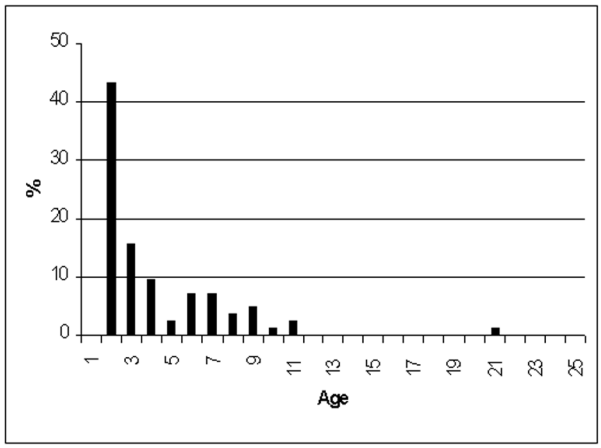


*Fig. 15. Results of fourth premolar age classes derived from Pike-Tay* et al. *(2000).*

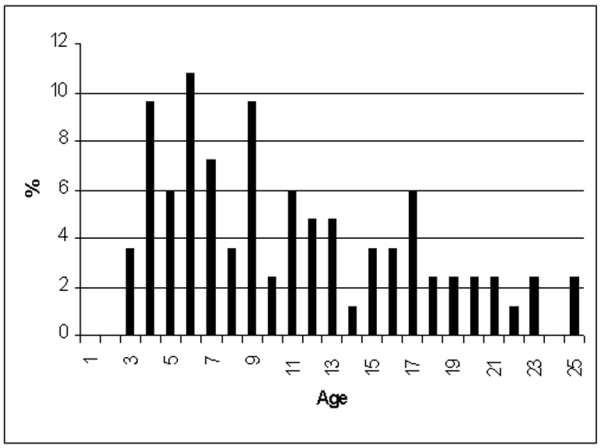


*Fig. 16. Results of fourth premolar age classes derived from the revised formulae for Verberie crown heights.*

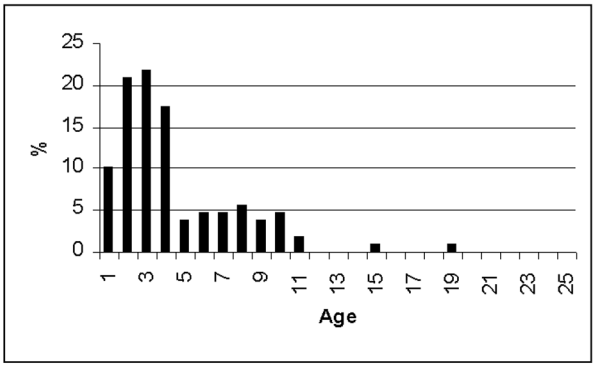


*Fig.17. Results of averaged individual age classes derived from Pike-Tay* et al. *(2000) for all permanent teeth averaged for each individual.*

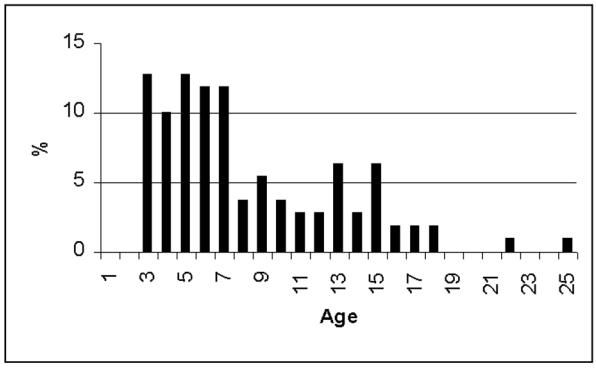


*Fig. 18. Results of averaged individual age classes derived from the revised formulae for Verberie crown heights for all permanent teeth averaged for each individual.*

numbers as age increases, with the exception of surprising peaks at 11 and 14 years. Maximum age extends to 25 years.

Sample size for the fourth premolar is slightly larger (n=83) than that for the third. Miller's (1974) data indicate 95% deciduous teeth at 22 months, and as much as 19% at 27 months. All were permanent teeth in occlusion by 29 months. For the Verberie assemblage, all should belong to the third or later year cohort. Pike-Tay *et al.* (2000) use 24 months for the $P_4$ eruption date, identical with that used for the M3 and the P3, although the P4 appears to be even more variable and later than either of those teeth in eruption timing. The Pike-Tay formula gives almost identical results for the $P_4$ as for the $P_3$ (Fig. 15), again with the overwhelming proportion in the second year and decreasing proportions through the eleventh year. One lonely outlier indicates age up to 21 years. The revised formula (Fig. 16) indicates a substantially older population. None are in the first two year cohorts, as is appropriate with the seasonality information; the highest proportions from four to nine years, but substantial representation extends up to 25 years.

### *Averaged individual age estimations*

All of the individual permanent tooth age calculations were averaged for each refitted individual, and age profiles of the population were constructed using the two methods. Note that this compares only the permanent teeth. Juvenile individuals with both deciduous and permanent teeth were included, but those without measurable permanent teeth were excluded at this stage. This was done to compare the two formulae, which dealt only with permanent teeth.

The Pike-Tay formula (Fig. 17) yielded a concentration of individuals in the first four years, and a sharp drop after that, with fairly even proportions from five to ten years and a few old individuals up to 19 years.

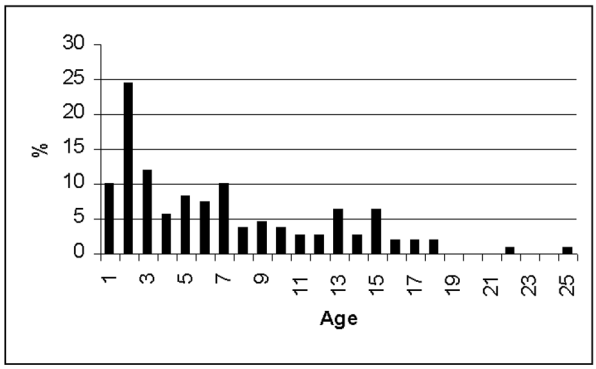


*Fig. 19. Results of averaged individual age classes from deciduous teeth and from permanent teeth derived from Pike-Tay* et al. *(2000).*

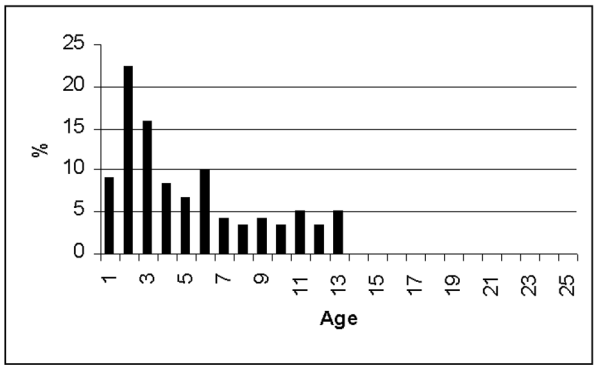


*Fig. 20. Results of averaged individual age classes from deciduous teeth and from permanent teeth derived from the revised formulae for Verberie crown heights.*

The revised formula (Fig. 18) yielded a mortality profile with a similar shape, but essentially shifted to older age ranges. It is strongly represented in the third through seventh year cohorts, then weakly represented in the eighth through eighteenth cohorts, with a very small proportion extending up to 25 years.

Since the mortality curves considered above were constructed by using only the permanent dentition, they cannot be considered to be representative of the full population represented by the faunal assemblage. The full sample was constructed by adding in first the juvenile individuals who did not have permanent teeth to be measured or considered in either mean age calculation adding in the juvenile deciduous dentition, and second, by reconsidering the ages of individuals with both deciduous and permanent dentition. It was previously mentioned that significant height variability in the youngest age classes might necessitate calculation of their age by other means (Pike-Tay *et al.* 2000). Deciduous wear and permanent eruption stages were used to place individuals in the first three age classes. Reassigned individuals were subtracted from the counts of individuals in age cohorts making up the mortality curve.

This did not significantly change the shape of the mortality curve for the Pike-Tay calculation (Fig. 19). It slightly reduced the proportions in the first two cohorts, and added to that of the third. The lack of many old individuals, and the strong representation in even the youngest cohorts, argue against calling this an attritional profile as taphonomic factors would have greatly reduced the preservation of the very young compared to the very old. This young-dominated mortality profile is essentially what had been previously reported for the Verberie assemblage using wear stages (Enloe 1997, 2001). The curve for the revised calculation (Fig. 20) does change fairly significantly from that in Fig. 18, particularly for the youngest cohorts. While the distribution of older individuals remains fairly similar, the first two cohorts are filled. The second year cohort has the highest proportion, and proportions decrease slowly with increasing age up to 18 years.

It is suspected that neither of these mortality profiles is correct. Clearly the original Pike-Tay *et al.* (2000) formulae with too-small original crown heights for the Verberie population over-represent the youngest cohorts. While the younger end of the population may be accurately estimated with the revised formulae, one must be quite sceptical of the extended age range, with substantial representation in the older age cohorts, up to 25 years. This dispersal of over-aged individuals is consistent with Gifford-Gonzalez's (1991) application of quadratic equations to bison control samples of known age.

It is suspected that substantial error in quadratic equations of any sort come in with the inclusion of premolars. These teeth are extraordinarily variable in their eruption sequence or timing. This can be seen in the numerous complete tooth rows in Verberie mandibles with quite similar eruption and wear in the permanent molars, but great differences in the presence, eruption state or wear of the premolars. They should probably be excluded from any mathematical calculations of age.

When only the molars are considered, are there differences in the results? The obvious first choice for analysis would be the first molar, the first erupting permanent tooth. It is present in individuals from three months of age, and has the longest period of use. The first molar also seems to yield age curves most at odds with the other molars, however. The $M_1$ yielded consistently greater ages than did the $M_2$ in individuals where both teeth were present and measurable. While the $M_2$ and $M_3$ ages were also variable within individuals, they were more frequently closer in age to each other than either of them to the $M_1$.

Gifford-Gonzalez (1991, 69) pointed out the statistical

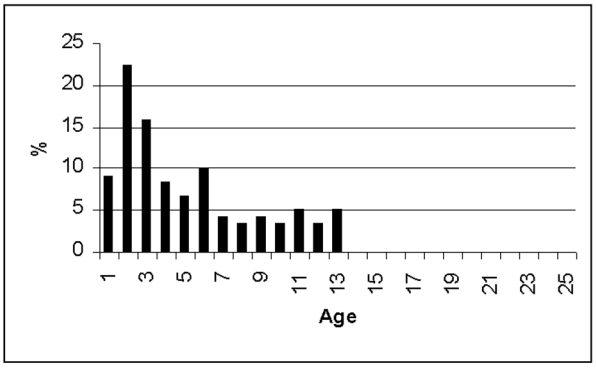


*Fig. 21. Mortality profile of age classes based on recalculated second and third molar crown heights and deciduous eruption and wear for the Verberie reindeer population.*

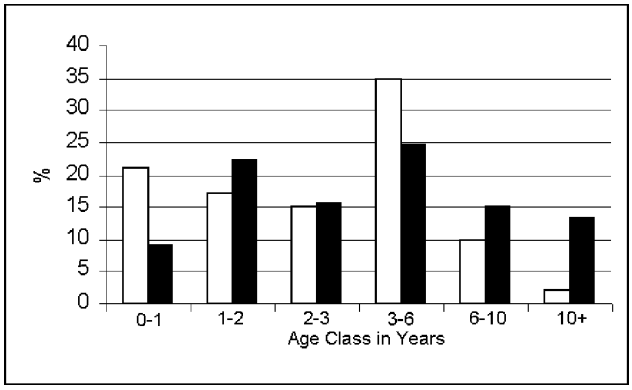


*Fig. 22. Comparison of proportions of age classes between the Verberie faunal assemblage (dark bars) and the living population (light bars) of the Nelchina herd (from Skoog 1968, 515).*

significance of underestimation of age by $M_1$ measurements of her two modern bison control samples. Perhaps for *Rangifer* this is because its wear is punctuated by the successive eruption and occlusion of the second molar behind it and then again by the replacement of the $D_4$ with the permanent fourth premolar. The timing of that second punctuation is, of course, apparently highly variable among individuals. It is probable that this tooth alone is responsible for the skewing of the Verberie mortality profile toward extreme age. When Gifford-Gonzalez (1991, 69) tested the fit between the actual and predicted ages of the individual molars of her control sample using Kolmogorov-Smirnov statistics, all of the individual molars yielded significant differences, except when combining the results from $M_2$ and $M_3$. Therefore, it seems reasonable to suggest that the ages of the individuals in the Verberie reindeer population might be most accurately estimated using the formulae for second and third molars adjusted for the empirically derived, original, unworn crown heights from the archaeological assemblage being studied. For the specimens that had those measurements possible, new ages were calculated for those individuals, then combined with the juveniles and other individuals for which new calculations were not possible. The results (n=121) are presented in Fig. 21.

Substantial proportions of young individuals, including juveniles and young adults up through the sixth year, characterize this new distribution. The proportion of older individuals is greatly reduced, particularly those of greater age. The maximum age is only thirteen years; this is consistent with the assumption of potential longevity of 200 months, or 16.67 years in both the Pike-Tay and revised formulae. Given the probably greater taphonomic affects on the very fragile first year cohort's remains, the mortality profile seems to resembles a catastrophic or living population age profile, with most numerous individuals of the youngest cohorts, and decreasing numbers of individuals with increasing age.

This final mortality profile is unfortunately made up of varying degrees of potential accuracy. Equivalent measurements were not available on all 128 individuals because the same number of teeth was not present in each of them. Nonetheless, it is probably the best overall calculation available from crown height analysis. This analysis has never been represented as determining the actual age of each tooth or individual, but rather as presenting the overall shape of the mortality profile, from which inferences about prey death and human hunting practices can be drawn.

This leads to a first interpretation that, with slight revisions, the original results from the wear stage analysis (Fig. 1) were not too far off base. While the population was probably not as young as the Pike-Tay formulae suggest (Fig. 4), it was not as old as the revised composite suggests either (Fig. 18). The distribution may be seen as essentially trimodal. There are clearly many young individuals, some of whom appear to be carrying deciduous teeth into the third year. There are also distinct peaks of young prime-age individuals, and of older individuals.

We may be able to evaluate the shape of the mortality profile by comparing it to the proportions of age groups in a sample of 1000 individuals from the modern Nelchina herd (Skoog 1968, 515). The age class categories have been collapsed into different groupings from those of the previous figures, because of the way the Nelchina data were collected and reported. While Fig. 21 suggests some similarity to the living population age structure, as noted above, Fig. 22 shows a number of discrepancies between the two distributions. At the outset, the first age group is represented in the Verberie sample at less than half of the proportion found in the Nelchina sample. At Verberie, these individuals are calves at four months of age (Enloe 1997), which are small, fragile specimens. Taphonomic

| Age class | Nelchina | | | Verberie | | | |
|---|---|---|---|---|---|---|---|
| | % | O | E | % | O | E | Total |
| 0–1 | 21 | 210 | 180.999 | 9.1 | 11 | 23.855 | 221 |
| 1–2 | 17 | 170 | 175.736 | 22.3 | 27 | 21.264 | 197 |
| 2–3 | 15 | 150 | 150.758 | 15.7 | 19 | 18.242 | 169 |
| 3–6 | 35 | 350 | 338.983 | 24.8 | 30 | 41.017 | 380 |
| 6–10 | 10 | 100 | 105.263 | 14.9 | 18 | 12.737 | 118 |
| 10+ | 2 | 20 | 32.114 | 13.2 | 16 | 3.886 | 36 |
| **Totals** | **100** | **1000** | | **100** | **121** | | **1121** |
| $X^2$=60.995**, significant for df=5, p<0.001 | | | | | | | |

*Fig. 23. Comparison of age groups between Nelchina herd and Verberie assemblage.*

factors probably account for the differences in this age category; there were undoubtedly substantially more first-year individuals in the original Verberie population. The second year cohort, aged at 16 months, is over-represented by more robust specimens, and may suggest that the Verberie sample originally contained a substantial proportion of animals from the two youngest age groups. The second discrepancy is in the group aged three to six years; the Verberie sample is again underrepresented. In the older age groups, and most particularly in the group over ten years of age, the Verberie sample is of a much greater proportion than that of the Nelchina sample. These differences can be evaluated with a chi-square test comparing the proportions of the age classes making up samples from the two populations (Fig. 23). These differences are highly significant ($X^2$=60.995**, significant for df=5, p<0.001) indicating very real differences in the mortality curves and suggesting significant differences from those previously proposed for the tactics or strategies of hunting reindeer at Verberie. The greatest discrepancies appear to be greater representation of the oldest individuals in the Verberie sample. If we consider that the youngest cohort probably had the most fragile specimens and are substantially under-represented for taphonomic reasons, the abundance of the second year cohort and the oldest cohorts suggests more of an attritional profile. This would mean less selective targeting of any individual age group and contradicts previous arguments for either prime-age dominant selection (c.f. Stiner 1991) or pre-reproductive juvenile and young adult selection for Verberie (Enloe 1997, 2001).

These results may well be an artifact of the methods employed, as were those of previously applied techniques. We will never know the past directly, but are always searching for methods to make our inferences more soundly based. The use of known-age control samples for the creation of formulae for age calculations and the comparison with the population structure of a sample of a living herd are both components of this effort to provide a methodologically sound basis for our interpretations. The methods proposed here, and the results achieved, emphasize the importance of studying individuals who compose the populations from which the archaeological samples are drawn, rather than merely studying them as isolated teeth.

## Problems and Biasing in Age Determinations of Horse: the Case of Solutré

The site at the base of the Roche de Solutré is, without a doubt, the most famous prehistoric site in Burgundy, France. Discovered on the 27th. September, 1866 by Adrien Arcelin (1881), excavations have revealed five cultural levels (Mousterian, Aurignacian, Gravettian, Solutrean and Magdalenian) in the thick deposits preserved at Solutré (Combier 1956, 1976). The repeated use of the locality from the Middle Paleolithic through to the end of the Upper Paleolithic is reflected through the archaeological evidence. During the Upper Paleolithic, horses dominated the faunas to such an extent that Solutré has been considered the "best preserved example of a large-game kill-site in Western Europe" (Olsen 1989, 295).

In 1994, a co-operative project was arranged between the excavator of the site, Jean Combier, the Service Régionale de l'Archéologie in Dijon and the Römisch-Germanisches Zentralmuseum Mainz, Forschungsbereich Altsteinzeit in Neuwied. The aim of the project was to characterise the type of faunal assemblage found at a Magdalenian kill and butchery site. The material analysed came from Magdalenian levels revealed during excavations in two areas – a small site ($2m^2$) in sector I11 and a larger site ($95m^2$) in sector P16. The faunal assemblages from both sectors were dominated by numerous remains of horse (Turner 1996, 2002).

In accordance with modern archaeozoological studies, age determinations of horse teeth from both sites were

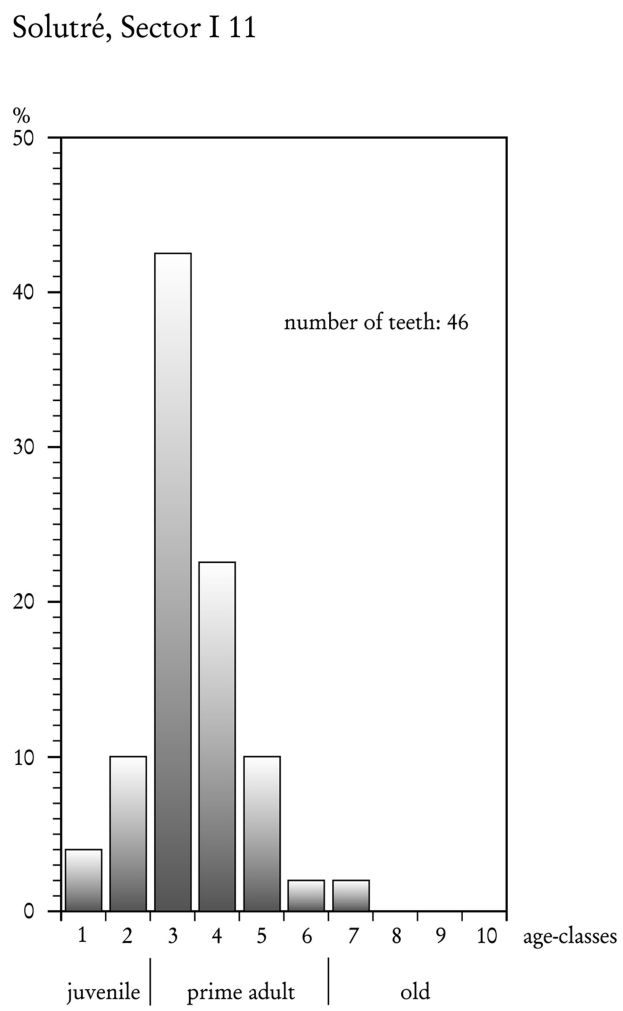


*Fig. 24. Histogram depicting the mortality profile of horses from sector I11 at Solutré. Single tooth measurements are expressed as percentages of the total number of teeth aged (n=46) in each age-class. For definitions of age-classes and juvenile, prime adult and old adult groups see text.*

undertaken, beginning with sector I11. The sample from this small site consisted of only 32 upper and 7 lower permanent premolars and molars, and 7 deciduous premolars. The permanent teeth were aged using Levine's crown height method (1979; 1982). Wear stages published by the same author were used to age the deciduous teeth. The single tooth measurements were plotted in age-classes as percentages of the total number of teeth aged (n=46) (Fig. 24). Each age-class represents 10% of the life-span, which was set at 20 years (Klingel and Klingel 1966), since under natural conditions equids older than 20 years of age would be rare (Levine 1979) or represented by only 2–3% of the natural horse population (Mohr 1971; Schaller 1972; Tyler 1969).

Stiner (1990) defined three different age-classes – juvenile, prime adult and old – for her assessments of mammalian mortality patterns. She defines "juveniles" as from birth to the age at which a particular taxon-dependent deciduous tooth is shed (approximately the first 20% of the natural longevity according to Lyman (1994)). "Prime adult" is the breeding age and "old" are adults past their prime (approximately the last 30% of the natural longevity (Lyman 1994)). These criteria were applied to the age-classes in the sample. The juvenile class was defined as from birth to the age at which the last deciduous cheek tooth in the horse, the $dp_4$, is lost (3½–4½ years according to Levine (1979; 1982)). Using Lyman's method of calculation, the first 20% of the natural longevity of horse used here is four years, which compares well with the range given by Levine for the $dp_4$. Thus, the boundary from the juvenile to the prime adult age-class was placed between age-classes 2 and 3 (2–4 and 4–6 years). Prime adults range from age-class 3 to age-class 7 (4–6 and 10–12 years). Old animals, representing the last 30% of the natural longevity, occupy the age-classes 7–10 (12+ years).

The resulting age-profile (Fig. 24) was dominated by horses in age-classes 3 (4–6 years) and 4 (6–8 years). These are young prime adult animals and about 78 % of the teeth in the sample were in this group. Approximately 14% of the teeth could be attributed to juveniles and only one tooth (2% of the sample) was from an old adult. The mortality profile appeared to show an excellent example of Magdalenians hunting with an eye for prime adult horse meat. The extremely high peaks in stage 3 and stage 4 were attributed to chance biasing in a small sample.

Since the sample of teeth was small, a more detailed ageing analysis, focusing on upper permanent premolars and molars, and in particular the third upper molar, was undertaken. The total of 12 third molars were sorted to left and right sides of the body and attributed to individual horses by comparing tooth morphology and crown wear and eruption stages. Several of the third molars belonged to intact or partially preserved rows of teeth, found either together during excavation or reconstructed during analysis. Altogether, nine individuals could be reconstructed and they are depicted schematically in Fig. 25 beginning with the youngest individuals at the top. The individuals were aged using comparative crown heights, eruption and tooth wear stages and stages of root development data given by Levine (1979; 1982).

The upper $M^3$'s of individuals I and II are unworn and root development has not begun. According to Levine (1979; 1982), the upper $M^3$ is in the unworn stage any time between 2–4½ years, but since root development in this tooth does not commence until the second year, these individuals were probably closer to 2 years of age at death.

Although the third molar of individual III shows the

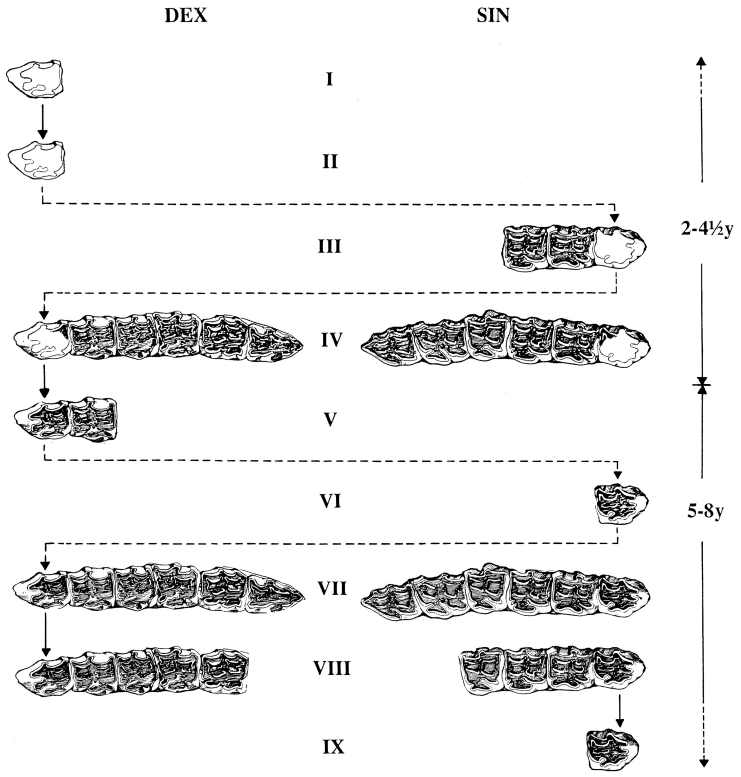


*Fig. 25. Schematic depiction of the dental series of nine aged individuals (I–IX) of horse from sector I11 reconstructed from upper permanent premolars and molars. The teeth are shown with occlusal surfaces uppermost; blank teeth represent unworn molars, filled teeth represent premolars and molars in wear. Approximate ages are given right.*

same stage of wear and root development observed in the molars of individuals I and II, its designation to one of these horses could be excluded since the tooth has a different pattern of enamel foldings on its occlusal surface. Individual III also possesses $M^1$ and $M^2$. Both teeth are slightly worn, a stage reached between 9 months and approximately 2 years. The fourth individual is slightly older, with first traces of wear on the anterior portion of the $M^3$. Unworn first and second incisors (not depicted in Fig. 25) were found together with these premolars and molars, suggesting death between 1½ and 4 years for individual IV.

Thus individuals I–IV are juveniles which appear to have been younger than 4½ years of age (= latest timing of unworn stage of $M^3$) at death. Individuals V–IX are adults aged between 5 and 8 years according to crown heights and wear stages of the teeth.

When the prime dominated, conventional mortality profile was compared with the schematic depiction of the aged individuals; it became clear that plotting measurements of single teeth – particularly from the dental series of individuals IV, VII and VIII – had enhanced counts in several age-classes out of proportion. Furthermore, discrepancies were observed between ages obtained from crown heights and ages obtained from eruption and wear stages. Individual IV is an example of this. Crown heights place the bulk of the teeth from this horse into the young prime adult category (age-class 4), but tooth eruption and wear patterns indicate that this animal died as a juvenile younger than four years of age.

In contrast to the conventional mortality profile, ageing individuals from the sample produced a mortality profile where juveniles and adults, with 4 and 5 individuals respectively, were more or less equally represented. Obviously there were problems with these results: only upper premolars and molars had been selected to reconstruct individuals, upper deciduous teeth, which might have increased juvenile representation, had been deliberately omitted, and there was no evidence for old adults, due to the absence of very worn third molars in the sample.

Unfortunately, time was too limited to undertake a detailed ageing analysis of the sample of teeth from the larger site in sector P16 due to the closing of the project in 1997. Conventional single tooth measurements of 232 horse teeth from this sector produced a mortality profile dominated once again by prime adults, with low numbers of juveniles and old adults (Fig. 26).

In 1997, Müller and Morel published their report on faunal remains from Hauterive-Champréveyres, a

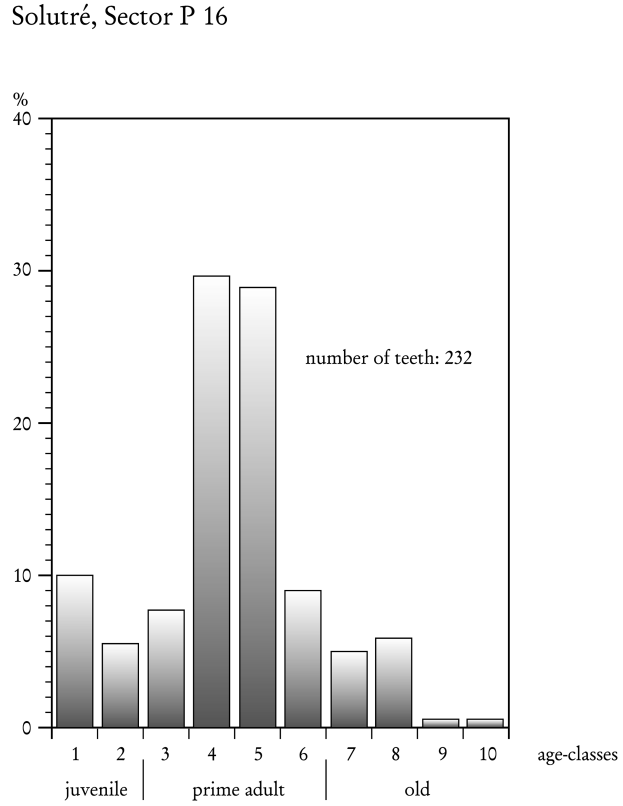


*Fig. 26. Histogram depicting the mortality profile of horses from sector P16 at Solutré. Single tooth measurements are expressed as percentages of the total number of teeth aged (n=232) in each age-class. For definitions of age-classes and juvenile, prime adult and old adult groups see text.*

Magdalenian site located on the northwest margin of Lake Neuchâtel in Switzerland. Horse is the most important species at this site and was the subject of a detailed analysis.

Using 179 upper and lower, deciduous and permanent, incisors, premolars and molars, Morel and Müller were able to reconstruct the dental series of at least 18 and possibly 21 different individuals of horse. The individuals were aged using data published by Habermehl (1961) and by Levine (1982).

The mortality profile of the horses from Champréveyres is characterised by a high proportion of juveniles younger than three years, absence of horses aged 4 and 5 years and low numbers of adults between 6 to 10 years (Fig. 27). Morel and Müller saw this mortality pattern as resulting from "attritional" hunting, where the least experienced, slower animals were preferably killed.

They also pointed out that a conventional single-tooth ageing analysis would have produced a mortality profile with a dominance of adults, a result which was not compatible with the profile produced by ageing individuals, where horses younger than three years of age dominated. Even more interesting was that the discrepancies observed between single tooth measurements and aged individuals in the selected, small sample of teeth from sector I11 were also cropping up in the non-selected, comparatively large sample of teeth from Champréveyres.

Thus, independent analyses of horse teeth from two Magdalenian sites indicate that single tooth measurements tend to enhance out-of-proportion counts of adult horses. So why does this happen? Histograms of single tooth measurements simply reflect the numbers of teeth

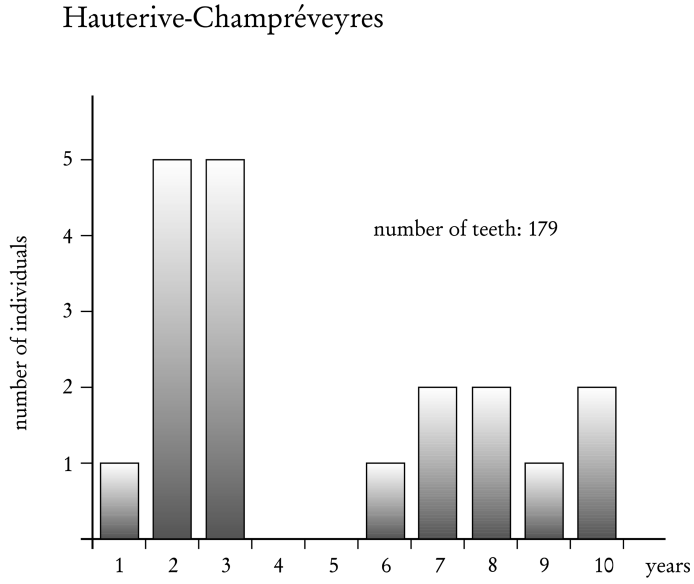


*Fig. 27. Mortality profile of aged individuals of horse from the Magdalenian site of Hauterive-Champréveyres in Switzerland (after Morel and Müller 1997, fig. 45).*

preserved in an assemblage that can be aged. In the case of the assemblages from sectors I11 and P16 at Solutré, counts of permanent teeth in various stages of wear well outnumbered counts of deciduous teeth. Is this a case of the differential preservation of immature and mature dentition? Levine (1983, 31) suggested that the incomplete mineralization of immature jawbones and teeth would likely result in the under-representation of juvenile teeth in fossil assemblages, and similar factors were suggested for Champréveyres. The preservation of teeth may be something that we have to look into in more detail in future.

Ageing individuals from sector I11 at Solutré shows that juveniles and adults may have been present in more or less equal numbers. Obviously at this point aged individual data from a larger sample at Solutré would be useful, the sample from sector P16 for example. Nevertheless, the provisional results indicate that juveniles and adults were present at this site in different proportions than previously thought.

For Solutré this may mean that we have to reconsider previous interpretations of horse mortality profiles, where it was suggested that lower proportions of juveniles and higher proportions of adults could reflect the selective killing of adult horses and releasing of young horses while they were held in a corralling situation in the cul-de-sac at the base of the cliff of the rock (Olsen 1989; 1995), or could reflect the exploitation of mainly adults in family groups of horses which were ambushed as they skirted around the base of the rock (Turner 2002).

## Conclusion

The results of dental studies of Verberie and Solutré indicate that mortality profiles determined from measurements of single teeth may yield misleading results in the proportions of adults and juveniles. Methods that employ tooth rows or dental series from identified individuals offer more reliable estimations of population age parameters than do those exclusively drawn from studies of single teeth.

How might these methods be most practically implemented archaeologically? We suggest that this might be best done in cases with well-preserved dental material, that is, those with intact or partially preserved rows of teeth. When the majority of dental material consists of loose individual teeth, it is generally a function of taphonomic processes, which also greatly affect the postcranial skeletal material. Information from mortality profiles and inferences about hunting strategies or tactics would be most useful when they can be integrated with reliable data on identifying sex, seasonality andparticularly differential element representation (e.g., Speth 1983). Thus, the most suitable material will probably be recovered from carefully excavated sites showing little evidence of disturbance, such as Solutré, Gönnersdorf or Pincevent.

This does not mean, however, that ageing of individuals would be impractical in other situations. A modified version of the aged individual method – establishing a series of individuals using crown height measurements of a single dental element for example – could be applied to assemblages recovered from fluviatile/semi-fluviatile/heavily disturbed deposits, and possibly teeth from old collections, where the requirements for reconstructing dental series may not be fully met. This could possibly produce results more reliable than single tooth measurements alone, but this idea needs to be tested further. There is obviously a danger that total numbers of individuals established for each element might be low, some age-groups might be over or under-represented.

A practical consideration is whether we should use only reconstructable individuals and discard the data on age in the remaining loose teeth. If the number of remaining loose teeth is small, and if their age-data are included in the ages of the individuals anyway, then they might be discarded (as Turner is currently doing with material from Gönnersdorf). The danger could be possible loss of data. If, for some reason, all the senile animals are represented by isolated teeth and there are no senile animals among the aged individuals, then obviously the data from the loose teeth will have to be incorporated into the age-profile for the assemblage. This problem could be overcome by including as many loose teeth as possible into the aged individual series, as was done for Sector I11 at Solutré. At Verberie, 128 individuals were identified from 380 mandibular specimens.

While there are still methodological problems to be resolved in individual tooth age determinations, we consider that ages of identified individuals, determined from a number of teeth, may yield more accurate mortality profiles of prey populations, and may lead to re-evaluation of scenarios of exclusively prime-age prey selection by technologically superior Upper Paleolithic hunters.

*Acknowledgements*

The authors would like to thank Deborah Ruscillo for not only making "Ageing and Sexing" an interesting and well-organised session, but also for successfully compiling and editing the papers for publication. Jim Enloe would like to acknowledge the financial support from the College of Liberal Arts and Sciences during his tenure as Dean's Scholar and from an Arts and Humanities Initiative grant from the Office of the Vice President for Research, University of Iowa, for making the research for this paper and its presentation at the ICAZ meetings in Durham. A travel grant from INSTAP

also aided in attending the conference. Elaine Turner would like to thank Regina Hecht (Monrepos) for preparing the figures and Jim for putting the paper together.

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*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 145–154*

# 9. A Bayesian Approach to Ageing Sheep/Goats from Toothwear

*A. R. Millard*

*For the last 20 years the human osteology literature has contained discussions of statistical problems with traditional skeletal ageing methods, which lead to "age mimicry", where the estimated age structure partly resembles that of the reference population. This paper discusses how these problems also apply to animal ageing techniques and proposes a method to overcome them in the case of ageing of sheep and goats by toothwear. A form of transition analysis is developed, using the data of Deniz and Payne as a reference population. The method is tested with other published known age animals. Payne's A–I mandible wear stages are investigated and found to underestimate variability. The method is applied to the large assemblage of sheep and goat mandibles from Arene Candide, Italy to illustrate the extent of uncertainty in estimating survivorship curves. The limitations of the current model and possible improvements are discussed.*

## Introduction

Ageing studies of both humans and animals rely on similar sets of changes in teeth and bones, yet there is little crossover between the zooarchaeological literature and the human osteoarchaeological literature on this topic. In the last 20 years, discussions of any method of ageing human skeletal material have been incomplete without reference to the important paper of Bocquet-Appel and Masset (1982), and the subsequent debate in the literature on how one estimates an age from an observed osteological state (Hoppa and Vaupel 2002). However, despite its relevance and importance I have been unable to find any mention of this paper in the zooarchaeological literature (for example, there are no citations in *Environmental Archaeology*, animal bone papers in *International Journal of Osteoarchaeology* (1995–2002), or the proceedings of the 1988 and 1994 ICAZ conferences in *Anthropozoologica*). This paper seeks to improve animal age estimation by bringing some of the cutting edge statistical methodology of human osteology to bear on animal ageing problems. It adopts a method known as 'transition analysis' (Boldsen *et al.* 2002; Millard and Gowland 2002) to estimate the age of sheep and goats from their toothwear, using the data of Deniz and Payne (1982) as a reference population. This approach is applied to the sheep and goat toothwear data from Arene Candide (Rowley-Conwy 1997) in order to obtain kill profiles which include estimates of the uncertainty due to both the ageing technique and sampling error.

## The Statistics of Ageing Techniques

Almost all skeletal ageing methods (both animal and human) have a common basis in their construction. The age indicator is observed in a modern *reference population* to establish its variation with age, and this information is then used to estimate the age of an archaeological *target population*. However, a number of studies of the past two decades have demonstrated that, unless particular care is taken, the age distribution of the target population will be affected by the age structure of the reference population (e.g. Bocquet-Appel and Masset 1982, 1985, 1996; Konigsberg and Frankenberg 1994; Konigsberg *et al.* 1997; Lucy *et al.* 1996; Aykroyd *et al.*

1997, 1999). This effect is termed "age mimicry". The key points that have been established are:

1. that age mimicry is a result of the inappropriate use of likelihood-based statistical methods to estimate the age of individuals (Konigsberg and Frankenberg 1992; Aykroyd *et al.* 1999), and is only absent when the reference population and target population have the same age structure, or the reference population is carefully constructed to have a uniform distribution of ages;
2. that the extent of age mimicry is inversely related to the correlation between the indicator and age (Aykroyd *et al.* 1997), that is, the more closely changes in the indicator are related to age, the less age mimicry will occur (and vice versa);
3. that the ages of individuals may be estimated reliably if Bayes' theorem is used to incorporate the prior probability of age based on the age structure of the population from which the individual is drawn (Konigsberg and Frankenberg 1994; Lucy *et al.* 1996);
4. that given (3), if we do not know *a priori* the characteristics of the population, then the problem is how to estimate the age structure of the population before (or simultaneously with) estimating the ages of the individuals (Hoppa and Vaupel 2002).

Ageing techniques for animal remains have proceeded on essentially the same basis as human ageing techniques traditionally did. They are therefore subject to the problems described above and also suffer from a lack of a full consideration of uncertainty:

> "nearly all methods of ageing in current use do not make proper use of the statistical nature of age estimates… age estimation from one or more skeletal traits is a process of generating the distribution of possible chronological ages....by throwing out distributional information around the mean or median age, we gain a false sense of statistical power about statements based on that age" (Konigsberg and Holman 1999, 265).

Traditional age estimation methods tend to treat ages as though they are exact, rather than a *distribution* of possible ages. However, no ageing method can produce exact chronological ages because individuals vary in the age of attainment of a given developmental or degenerational stage. Even if an indicator was perfectly correlated with chronological age and all variation eliminated, the use of an ordinal scoring method (as for tooth development and toothwear) *still* yields a distribution of ages rather than an exact age because individuals enter a given stage and remain there for some period of time (Konigsberg and Holman 1999).

Some zooarchaeological workers have recognised the uncertainty of ageing and compensated for it by using broad categories such as "immature" (e.g. O'Connor 1991) or simply wear stages (e.g. Jones 1992). Even these procedures are problematic. Use of broad age categories takes the detailed age structure evidenced in toothwear and other skeletal indicators and discards it because the detail is difficult to interpret. Use of the indicator states alone allows comparison between assemblages for similar or dissimilar survival patterns, but does not allow these patterns to be related to theoretical concepts such as Payne's (1973) milk, meat and wool survivorship curves. In recent years in order to address these problems, there has been a move in human osteoarchaeology towards the use of Bayes' Theorem for age estimation. For this purpose, Bayes' theorem may be represented by the following equation:

| posterior probability of having age $a$ given the observed osteological state | $\propto$ | likelihood of being in the observed state, $c$, if we knew the age was $a$ | $\times$ | prior probability of having age $a$ |
|---|---|---|---|---|

$$p(a|c) \propto p(c|a) \times p(a)$$

where $a$= age, and $c$= indicator (e.g. toothwear stage)

Several age indicators (e.g. the state of different teeth) can easily be combined if we assume that while they are conditional on age, they are independent of each other given age. This is advantageous when estimating age from multiple variables and automatically weighs each indicator according to the probability distribution, eliminating the dubious process of imposing weights, or worse still, assuming that each indicator contributes equally (Lucy 1997).

In the application of Bayesian statistics to palaeodemography, the choice of prior is crucial. For example, Lucy (1997) adopts a prior based on the age distribution of the reference sample, but this incorporates a bias inherent in regression analysis, and better priors can be chosen. In contrast, Chamberlain (2000) compares the adoption of a uniform prior on age and a prior based on model life tables. A further development has been that of estimating the structure of ages in the population from the distribution of indicator states in the population (Love and Müller 2002; Holman *et al.* 2002) using the principle of maximum likelihood to obtain a single age structure which can be used as a prior for the estimation of individual ages. However, there is clearly going to be some uncertainty about what age structure, and Konigsberg and Herrman (2002) take the further step of considering the distribution of probabilities of age structures given by the likelihood in their age estimation. In this paper, I take a different approach by including a Bayesian (rather than likelihood) consideration of the distribution of age structures. This extends the method of Chamberlain (2000) by considering a prior *range* of age structures, themselves with varying probabilities, based on theoretical considerations, in this case Payne's idealised kill patterns for milk and wool economies.

## Materials and Methods

### *Data*

Several sets of previously published data are analysed in this paper. First, the data of Deniz and Payne (1982) on tooth eruption and wear in Turkish Angora goats are analysed as a reference population. Their study is by far the largest on tooth eruption and wear in sheep or goats, and the data are published fully enough to allow re-analysis. Deniz and Payne analysed their data to estimate transition ages and their variability assuming that the cumulative percentage of individuals having attained or passed a particular stage was log-normally distributed on an age scale starting at birth. Here I assume that the cumulative percentages are log-logistically distributed with respect to age from conception. A logistic distribution is used in preference to a normal distribution because:

a. it has heavier tails which help to counter the problem of underestimating uncertainty by assuming all of an individual's tooth eruption and wear states are independent given the animal's age;
b. it is computationally more stable in the software package used (WinBUGS) than the common alternative cumulative normal distribution.

Gestation in sheep is 147 days (Blaxter 1980, 9), and I assume the same for goats, which have gestation of about five months (Dahl and Hjort 1976, 92). Any difference will have little influence on estimated ages apart from those of the very youngest animals. The use of data on goats to produce an ageing technique for sheep needs some justification. The available data on tooth eruption timing in sheep and goats (summarised in Hillson 1986, 202–203) suggests little difference between the species, but see the discussion in Jones (this volume) for a consideration of possible differences. The tooth morphology is so similar that although the species can be distinguished on the basis of the cheek teeth when fully erupted and not heavily worn (Payne 1985; Halstead *et al.* 2002), the same eruption-attrition schemes are necessarily used for both (Hillson 1986, 202). "This leaves the question of applying data from Turkish goats to archaeological sheep: the close phylogenetic relationship of the species, and the general similarity of dental development in sheep and goats, give some reason to accept the results of such a comparison." (Moran and O'Connor 1994, 269)

Secondly, the ageing method is tested on the data from known age sheep presented by O'Connor (1998), and finally it is applied to the recorded toothwear of sheep and goat mandibles from the Early Neolithic (n=50) and Middle Neolithic I (n=283) levels at Arene Candide, Italy (Rowley-Conwy 1997). The latter two data-sets consist, as in many archaeological assemblages, of data on the cheek teeth only, i.e. the deciduous fourth premolar and its replacement the permanent fourth premolar, and the first, second and third molars (denoted dp4, P4, M1, M2 and M3 respectively). Therefore, only these teeth from the Deniz and Payne (1982) data are included in the first analysis.

### *Mathematical/Statistical models*

As tooth eruption and wear are recorded as a series of ordinal stages, I adopt a model based on analysing the threshold age of (or age of transition to) a stage, and the variability between individuals of that threshold, to obtain the probability that a tooth is in a particular stage. The model described below is very similar to that developed by Millard and Gowland (2002) for the analysis of tooth development and wear in humans, and is a form of transition analysis analogous to those of Boldsen *et al.* (2002) and Holman *et al.* (2002) for other ordinal age indicators in humans.

If $Q_{ijk}$ is the probability of tooth $j$ of individual $i$ having passed the threshold for the end of stage $k$ ($k$= 1,2,….$N_j$-1, where $N_j$ is the number of stages for tooth $j$), then

$$\text{logit}\,(Q_{ijk}) = \delta_j \times (\ln(\theta_i) - \ln(\gamma_{jk})) \qquad (1)$$

Where $\text{logit}(Q) = \ln(Q/(1-Q))$, $\theta_i$ is the individual's age, $\gamma_{jk}$ is the mean threshold age for the tooth and stage in the population, both expressed as years from conception and $\delta_j$ is the discriminability, which measures how close together the transitions in the population are. If $p(k_{ij} \mid \theta_i)$ is the probability of tooth $j$ of individual $i$ being in stage $k$ at age θ, then:

$$p(1_{ij} \mid \theta) = 1 - Q_{ij1}$$
$$p(k_{ij} \mid \theta_i) = Q_{ijk-1} - Q_{ijk} \text{ for } 2 \le k \le N_j - 1 \qquad (2a)$$
$$p(N_{ij} \mid \theta_i) = Q_{ijN_j-1}$$

In the case of the two teeth dp4 and P4 the observation of a state of wear on dp4 is conditional on P4 not having erupted. Thus, for dp4 the above equations are modified so that:

$$p(1_{i,\text{dp4}} \mid \theta_i) = (1 - Q_{i,\text{dp4},1}) \times p(1_{i,\text{P4}} \mid \theta_i)$$
$$p(k_{i,\text{dp4}} \mid \theta_i) = (Q_{i,\text{dp4},k-1} - Q_{i,\text{dp4},k}) \times p(1_{i,\text{P4}} \mid \theta_i) \text{ for } 2 \le k \le N_{\text{dp4}} - 1 \qquad (2b)$$
$$p(N_{i,\text{m3}} \mid \theta_i) = Q_{i,\text{m3},N_{\text{m3}}-1} \times p(1_{i,\text{P4}} \mid \theta_i)$$

By specifying a joint likelihood for the data, we are able to provide a full probability model for all observable and unobservable quantities (Lunn *et al.* 2000). If we assume that the wear stages of all the teeth are independent, then:

$$p(\mathbf{k}_i \mid \theta_i) = \prod_j p(k_{ij} \mid \theta_i)$$

Where $\mathbf{k}_i$ is the set of observed stages for individual $i$. Note that if the assumption of independence does not hold, then this method will underestimate the uncertainty in age. In order to make inferences about age, we use

Bayes' theorem to construct the posterior distribution from the observed data.

$$p(\theta_i \mid \mathbf{k}_i, S) \propto p(\mathbf{k}_i \mid \theta_i) \times p(\theta_i \mid S)$$

However, this is entirely conditional on knowing the age structure of the population, *S*. At the population level we may write, using Bayes' theorem again:

$$p(\Theta, S \mid \mathbf{K}) \propto p(\mathbf{K} \mid \Theta, S) \times p(\Theta, S)$$

where $\Theta$ is the collection of ages in the population, and **K** is the entire set of observed stages in the population. Hence,

$$p(\Theta, S \mid \mathbf{K}) \propto p(\mathbf{K} \mid \Theta) \times p(\Theta \mid S) \times p(S)$$

As the ages of the individuals are independent given *S*,

$$p(\Theta, S \mid \mathbf{K}) \propto \prod_i [p(\mathbf{k}_i \mid \theta_i) p(\theta_i \mid S)] \times p(S)$$

In order to apply this model, it is necessary to determine the values of the mean thresholds and the discriminabilities, observe a set of toothwear states, and provide prior probabilities for the possible age structures.

Because the joint posterior distributions in these equations require complex numerical integrations, I use a Markov-chain Monte Carlo (MCMC) method for its evaluation using the WinBUGS program (Spiegelhalter *et al.* 2000; Lunn *et al.* 2000).

The code used is available from my website http://www.dur.ac.uk/a.r.millard/BUGS4Arch.html.

### *Subsidiary model for reference data*

A modification of the above model is required to handle all of the observations of Deniz and Payne (1982). In some cases they were unable to observe the actual wear stage of a tooth, but instead they report that the tooth is in one of two possible wear stages. This was attributed to the lower light levels in winter and the reduction in light available for examination of the rear cheek teeth. I shall term these "grouped stages". Grouped stages do not occur at random, so simply discarding the data is likely to lead to biased estimated of the transition parameters. We therefore require a mathematical description of how they occur, the parameters of which can be estimated along with the transition parameters.

If a tooth is observed as in either stage *k* or *k*+1, the observed state is denoted *k**. Its true state is either *k* or *k*+1. The probability of being unable to distinguish the two wear stages will depend on the true wear stage, and the time of year, or equivalently the age of the animal (as following Deniz and Payne (1982), the births are all treated as occurring on 1 April). We therefore write:

$$p_{obs}(k^* \mid k, j) = p_{k,j+} \times \beta \quad \text{and} \quad p(k^* \mid k+1, j) = p_{k,j-} \times \beta \quad (3)$$

where $p_{k,j+}$ and $p_{k,j-}$ represent the probabilities of confusing a stage with the succeeding or preceding one respectively under optimum lighting conditions, and $\beta$ is a parameter to represent the varying effect of lighting conditions. We have no clear idea of how this might vary, but as a first approximation assume that it varies sinusoidally through the year, so that $\beta = \beta_{min} + \Delta\beta \times (1+\sin(\varphi+2\pi\theta))$, with $\beta_{min}$, $\Delta\beta$ and $\varphi$ parameters to be estimated. The probability of actually observing stage *k* is then reduced:

$$p_{obs}(k \mid \theta, p_{k,j+}, p_{k,j-}, \beta) = p(k_{ij} \mid \theta_i) - p_{obs}(k^* \mid k, j) - p_{obs}([k-1]^* \mid k, j)$$

Using equations 1, 2 and 3, a regression is performed on the data of Deniz and Payne (1982) to determine the unknown $\Gamma_j$ (the set of threshold parameters for tooth *j)* and $\delta_j$. In this case, Bayes' theorem is written:

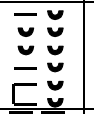
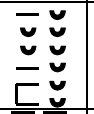
$$p(\Gamma_j, \delta_j \mid \mathbf{K}) \propto p(\mathbf{K} \mid \Gamma_j, \delta_j) \times p(\Gamma_j) \times p(\delta_j)$$

and is used to obtain probability distributions for the parameters, which are summarised in Fig. 1 as means and standard deviations. The priors assumed were uninformative, to express a lack of prior knowledge: the $\gamma_{jk}$ were assumed to be uniformly likely to lie between conception and 13 years after birth, subject to the constraint that they were ordered according to *k*. The other priors were: $\delta_j \sim$ Gamma(0.01,0.01) which constrains $\delta_j$ to be positive; $p_{k,j+} \sim$ Unif(0,1), and $p_{k,j-} \sim$ Unif(0,1) as probabilities must lie between zero and one; $\Delta\beta \sim$ Unif(0,1), $\beta_{min} \sim$ Unif(0,1- $\Delta\beta$), and $\varphi \sim$ Unif(0, $2\pi$) which simply constrain these parameters to the range of possible values.

### *Prior distribution for the age structure*

The final element of the model required for its application is the prior p(*S*) on the age structure. Clearly, the range of likely age structures must encompass Payne's (1973) idealised structures for milk, meat and wool economies. To represent these as parametric equations would require some terms to represent the natural mortality of sheep, with additional terms to describe the various possibilities for additional mortality from slaughter by humans. Wood *et al.* (2002) suggest that a model with at least five terms is required to describe natural mortality; it is likely that three more terms would be required to describe age-specific slaughter by humans (one each for mean age, variability of age and intensity of slaughter). Payne (1973) notes four ages when specific economies would require slaughter, and mixed economies might use all of them. An equation with at least 17 parameters is therefore required, and may not be adequate even then. Such a complex model will be difficult to specify and computationally expensive. For this reason, I adopt a discrete non-parametric approach, where the age range from conception to 13 years is approximated by 100 equally-spaced ages, $t_a$ (a=1..100) and the set of ages of the animals is treated as a multinomial draw from these 100 possible ages. The age structure ISI*S* is then expressed

*Fig.1. Stage codes and mean thresholds for exit of a stage (in years from birth) estimated from data of Deniz and Payne (1982). Uncertainties are given as one standard deviation.*

| | dp4 | | | | P4 | | | | M1 | | | | M2 | | | | M3 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stage number (this study) | Deniz & Payne (1982) symbol | Rowley-Conwy (1997) code | male threshold | female threshold | Deniz & Payne (1982) symbol | Rowley-Conwy (1997) code | male threshold | female threshold | Deniz & Payne (1982) symbol | Rowley-Conwy (1997) code | male threshold | female threshold | Deniz & Payne (1982) symbol | Rowley-Conwy (1997) code | male threshold | female threshold | Deniz & Payne (1982) symbol | Rowley-Conwy (1997) code | male threshold | female threshold |
| 1 | nye | V | 0.01 ±0.01 | 0.01 ±0.01 | | V | 1.76 ±0.02 | 1.79 ±0.03 | nye | V E H | 0.20 ±0.02 | 0.22 ±0.02 | nye | V E H | 0.88 ±0.02 | 0.88 ±0.02 | nye | V E H | 1.96 ±0.03 | 2.08 ±0.03 |
| 2 | E | E | 0.03 ±0.01 | 0.02 ±0.01 | E | E | 1.77 ±0.03 | 1.80 ±0.03 | UJ | U 1 | 0.33 ±0.02 | 0.32 ±0.02 | UJ | U 1 | 1.02 ±0.02 | 1.06 ±0.02 | UJ | U 1 | 2.12 ±0.03 | 2.24 ±0.03 |
| 3 | ½ | H | 0.05 ±0.01 | 0.06 ±0.02 | ½ | H | 1.85 ±0.03 | 1.90 ±0.03 |  | 2 | 0.48 ±0.02 | 0.46 ±0.02 |  | 2 | 1.22 ±0.02 | 1.26 ±0.03 | | 2 | 2.50 ±0.04 | 2.70 ±0.04 |
| 4 | UJ | U 1 | 0.06 ±0.01 | 0.08 ±0.02 | UJ | U 1 | 1.87 ±0.03 | 1.94 ±0.03 | | 3 | 0.52 ±0.02 | 0.55 ±0.02 | | 3 | 1.34 ±0.02 | 1.62 ±0.04 | | 3 | 2.71 ±0.06 | 3.06 ±0.06 |
| 5 | C1W | 2 | 0.07 ±0.02 | 0.10 ±0.02 | int | 2 3 4 | 2.30 ±0.03 | 2.43 ±0.03 | | 4 | 0.72 ±0.03 | 0.81 ±0.05 | | 4 | 1.79 ±0.05 | 2.07 ±0.04 | | 4 | 2.94 ±0.07 | 3.43 ±0.05 |
| 6 | C2W | 3 | 0.12 ±0.01 | 0.13 ±0.02 | | 5 6 | 2.54 ±0.03 | 2.70 ±0.04 | | 5 | 0.74 ±0.04 | 0.89 ±0.03 | | 5 | 1.90 ±0.03 | 2.13 ±0.03 | | 5 | 3.09 ±0.08 | 3.70 ±0.07 |
| 7 | C3W | 4 | 0.20 ±0.02 | 0.20 ±0.02 | | 7 | 2.89 ±0.06 | 3.26 ±0.04 | | 6 | 0.95 ±0.03 | 1.07 ±0.03 | | 6 | 2.31 ±0.03 | 2.58 ±0.04 | | 6 | 3.24 ±0.09 | 3.84 ±0.07 |
| 8 | | 5 | 0.34 ±0.02 | 0.39 ±0.02 | | 8 | 5.26 ±0.07 | 6.04 ±0.07 | | 7 | 1.26 ±0.03 | 1.34 ±0.03 | | 7 | 2.51 ±0.04 | 2.88 ±0.04 | | 7 | 4.09 ±0.10 | 4.27 ±0.07 |
| 9 | | 6 | 0.56 ±0.02 | 0.57 ±0.02 | | 9 | 9.52 ±0.23 | | | 8 | 2.83 ±0.07 | 3.30 ±0.05 | | 8 | 5.58 ±0.09 | 6.28 ±0.08 | | 8 | 4.35 ±0.10 | 4.64 ±0.07 |
| 10 | etc | 7 | 1.05 ±0.03 | 1.16 ±0.03 | etc | – | | | | 9 10 | 3.10 ±0.08 | 3.78 ±0.06 | | 9 10 | 6.03 ±0.12 | 6.86 ±0.08 | | 9 | 4.48 ±0.10 | 4.95 ±0.08 |
| 11 | | 8 9 | 1.25 ±0.03 | 1.41 ±0.04 | | | | | | 11 | 4.42 ±0.11 | 4.84 ±0.08 | | 11 | 6.18 ±0.13 | 7.76 ±0.10 | | 10 | 7.37 ±0.23 | 9.14 ±0.15 |
| 12 | | 10 11 | 1.42 ±0.03 | 1.57 ±0.04 | | | | | | 12 13 | 4.58 ±0.12 | 5.00 ±0.08 | | 12 13 | 6.23 ±0.14 | 8.05 ±0.11 | | 11 12 | 8.35 ±0.19 | 10.07 ±0.24 |
| 13 |  | 12 | | | | | | |  | 14 | 9.83 ±0.40 | |  | 14 | | |  | 13 | 9.26 ±0.24 | |
| 14 | | | | | | | | |  etc | – | | |  etc | | | |  | 14 15 | 9.68 ±0.30 | |
| 15 | | | | | | | | | | | | | | | | |  | 16 | | |
| δ | | | 12.7±1.0 | 10.6±0.8 | | | 29.6±2.6 | 20.5±1.3 | | | 14.5±0.9 | 14.6±0.7 | | | 25.1±1.8 | 18.2±0.9 | | | 22.1±1.8 | 16.6±0.9 |

as the set of proportions, $S_a$, of the underlying population with ages $t_a$. A prior for $S$ can then be constructed using a variant of the method of Adcock (1987). If we take Payne's milk and wool curves as two prior estimates of $S$: $\mathbf{e}_1$ and $\mathbf{e}_2$, then Adcock shows that a suitable prior for the proportions in $S$ is given by a Dirichlet distribution (a multivariate distribution expressing uncertainty about a set of proportions) with $\mathbf{h} = \frac{1}{2}(\mathbf{e}_1 + \mathbf{e}_2)$ as the mean prior estimate, and $C = 2(1 - \sum_a \eta^2_a) / \sum_a d^2_a$ is the "prior sample size", where $\mathbf{d} = (\mathbf{e}_1 - \mathbf{e}_2)$. Taking $\mathbf{e}_1$ and $\mathbf{e}_2$ from Payne's piecewise linear survivorship curves without additional interpolation gives C=26 and a prior with the 95% confidence range on the survivorship curve shown as a solid line in Fig. 2. However, the range of survivorship curves allowed by this prior is mostly between the Payne milk and wool curves, which is a rather narrow range compared to the variation seen in archaeological assemblages. A prior given by C=10 (Fig. 2, dotted line) seems more in line with our prior knowledge of the form of $S$.

## Results

### *Reference population data*

The threshold ages estimated from Deniz and Payne's (1982) data are shown in Fig. 1. The mean ages of transition for females obtained with this method are very close to those illustrated by Deniz and Payne (1982, fig. 24). The discriminabilities for both males and females decrease in the order P4, M2 M3, M1, dp4: this accords with the increases in variability noted by Deniz and Payne. Males are generally earlier than females in their mean transitions, but also exhibit less variability (higher discriminability) than females.

### *Known age animals test*

There is only a limited amount of published data on the state of wear of the complete set of teeth of individuals of known age suitable for testing the age estimates of the method. Deniz and Payne (1982) give tooth wear data for nine male goats aged 19 or 31 months, and, in addition, O'Connor (1998) gives tooth wear data for 32 modern reference collection sheep aged 5–6 months or 11–12 months (sex is not given). This collection of known age animals is far from a random draw from the age structure of a herd: in both cases, a group of animals has been selected to illustrate the range of variation in the state of the teeth at specific ages. It thus does not make any sense to try to estimate the age structure of the population from the data, and some form for $S$ must be assumed in order to estimate ages. In the case of Deniz and Payne, the animals are drawn from a deliberately constructed population with as near as possible the same number of animals in each age class, so an *a priori* assumption that all ages are equally likely is sensible. In the absence of any other evidence, this is also adopted as a neutral prior for O'Connor's data, though it is not particularly satisfactory.

The results of this test are shown on Fig. 3. Four of the 42 individuals have estimated 95% confidence ranges that do not include the known age. However, two of them are only just outside the range and we know that the assumption of independence of the state of teeth given age is likely to be violated so that the estimated confidence ranges are too narrow. The nine animals from Deniz and Payne (1982) were of course included in the data used to construct the model, and therefore provide less of a test than the data of O'Connor. The number of mis-aged animals is not too large given the known inadequacy of the model, and the application of goat data to sheep. The data do however illustrate the problem of lack of sex information: the difference in ages for males and females with the same tooth wear state increases with age.

### *Payne mandible wear stages*

Before examining a case study, it is instructive to consider what this model and transition age estimates imply about the mandible wear stages A–I given by Payne (1973). These are widely used and the equivalent ages given by Payne for these stages are used to compare archaeologically derived survival curves with Payne's three idealised curves for milk, meat and wool economies. Fig. 4 shows the small number of transitions that define Payne's mandible wear stages, and the estimates of the ages of male and female animals falling in each stage using only these transitions and a uniform prior, compared with the ranges given by Payne (1973). It is clear that the commonly used ranges are underestimates of the variability in age of animals in a stage, and that in the latter stages, the ages are underestimated, particularly for females. The age range for the final stage is rather dependent on what is assumed as the absolute upper age limit for sheep or goats (in this case 13 years was assumed).

### *Case study: Arene Candide*

The Arene Candide data have been analysed twice: once as if all individuals were female and once as if they were all male, as sheep and goat mandibles cannot be sexed. The results for the analyses are shown in Figs 5 and 6. The uncertainty in the survivorship curves is shown as the marginal 95% confidence limits at each age. It is clear that the bounds on the Early Neolithic survivorship include an idealised milk economy, as well as a variety of intermediate milk-meat economies. The Middle Neolithic I bounds are much more clearly intermediate between the idealised milk and meat economies. In both cases the

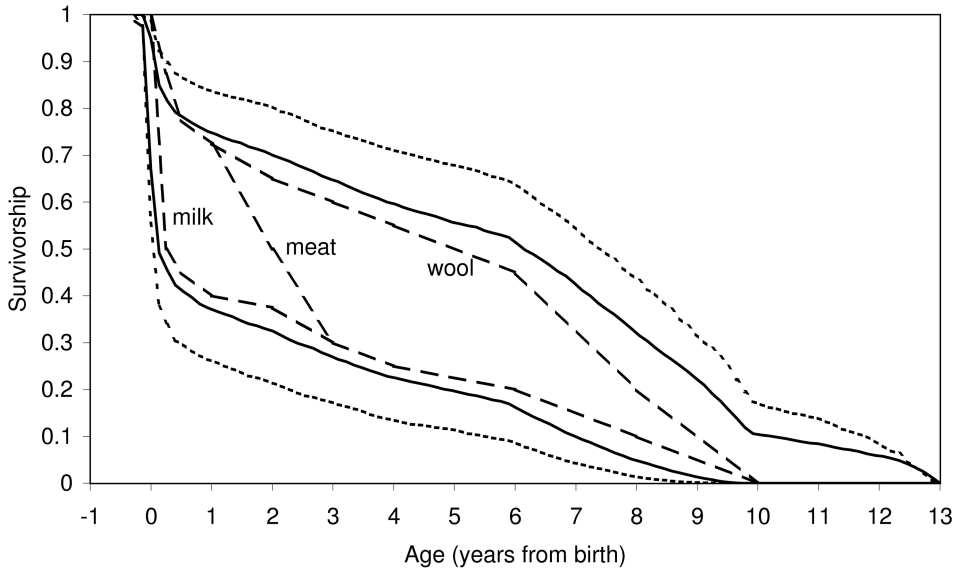



*Fig. 2. Prior confidence limits on the survivorship curve. Dashed lines: from top to bottom, Payne's (1973) wool, meat and milk curves. Solid line: prior 95% confidence limits by method of Adcock (1987). Dotted line: prior 95% confidence limits adopted here.*

survivorship falls off faster than would be predicted by any of the ideal curves once past the age of five or so. The Early Neolithic curve is significantly different from that derived by Rowley-Conwy using traditional methods and shows the effect of removing the under-ageing of those methods.

Both data-sets show that there are differences in the result depending on the sex of the animals. As the sex ratio is expected to vary with age in different ways with different economies, it is not possible to assume one sex ratio and adjust the spread of possible survivorship curves for the uncertain sex of each animal. Some data on the variation of sex ratio with age is needed. It might be sufficient to assume the sex ratio at birth and know the average adult sex ratio in order to do this, but more work would be needed to develop suitable statistical models.

There are distinct sections of all curves that show a rapid fall in survivorship, which could be interpreted as age-specific slaughter. However, if there is covariance in the ages of transition, and if there is a bunching of transitions in different teeth in a short age-span, then, when the transitions are treated as independent, there will be an underestimate of uncertainty which biases ages to fall one side or the other of the bunch of transitions. Such an effect could be causing the rapid falls in survivorship and demonstrate one of the fundamental weaknesses of having to assume independence because there are no data on covariance. If one were able to estimate the mean thresholds from the tooth wear states of individuals, it would be possible to allow for covariance of tooth wear stages. Hence, it must be concluded that even better reference data are needed than those of Deniz and Payne (1982). The data of Jones (this volume) look promising in that regard, and would also allow different age estimations to be established for sheep and goats.

The prior on the survivorship curve adopted here is only a crude approximation of our prior knowledge. A more realistic prior might be constructed by considering what range of kill profiles are compatible with maintaining herd reproductive potential, for example, using the simulation methods of Cribb (1985).

## Conclusions

This paper has shown that the statistical methods underlying skeletal ageing techniques for animals need to be overhauled. The proposed technique of transition analysis using Bayesian statistical models shows that this can be done. The examples analysed here show that there is great uncertainty in ageing of animals, especially as that shown here is certainly an underestimate. More work is needed to incorporate sex ratios into the estimation of survivorship curves. The methods presented have also ignored taphonomic biases: I have assumed that we have a representative sample of the target population. To consider taphonomic processes will require appropriate statistical models to incorporate into the analysis the additional uncertainty which they bring. Rogers (2000) method for 'Analysis of Bone Counts' is promising in this regard, but it demands carefully observed and recorded actualistic data of a type not widely available at the moment.

*Acknowledgements*
I am grateful to Peter Rowley-Conwy for supplying me

| Age (months) | Age (years) | | Ref | toothwear stage# | | | | | 95% confidence interval for age (years) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | dp4 | P4 | M1 | M2 | M3 | female | male |
| 5 | 0.42 | * | 1 | 10 | NA | 5 | 1 | 1 | 0.49–0.92 | 0.47–0.87 |
| 5.5 | 0.46 | | 1 | 9 | NA | 5 | 1 | 1 | 0.40–0.81 | 0.37–0.76 |
| 5.5 | 0.46 | | 1 | 9 | NA | 3 | 1 | 1 | 0.28–0.61 | 0.28–0.61 |
| 5.6 | 0.47 | | 1 | 8 | NA | 3 | 1 | 1 | 0.21–0.53 | 0.21–0.51 |
| 5.6 | 0.47 | | 1 | 9 | NA | 5 | 1 | 1 | 0.40–0.81 | 0.37–0.75 |
| 5.75 | 0.48 | | 1 | 9 | NA | 3 | 1 | 1 | 0.27–0.61 | 0.28–0.60 |
| 5.75 | 0.48 | | 1 | 9 | NA | 4 | 1 | 1 | 0.34–0.68 | 0.33–0.66 |
| 5.8 | 0.48 | | 1 | 9 | NA | 3 | 1 | 1 | 0.28–0.61 | 0.28–0.61 |
| 5.8 | 0.48 | | 1 | 9 | NA | 3 | 1 | 1 | 0.27–0.61 | 0.28–0.61 |
| 5.8 | 0.48 | | 1 | 9 | NA | 3 | 1 | 1 | 0.28–0.61 | 0.28–0.61 |
| 5.8 | 0.48 | | 1 | 9 | NA | 3 | 1 | 1 | 0.28–0.62 | 0.28–0.61 |
| 5.8 | 0.48 | | 1 | 10 | NA | 3 | 1 | 1 | 0.31–0.75 | 0.35–0.77 |
| 5.8 | 0.48 | | 1 | 8 | NA | 3 | 1 | 1 | 0.22–0.53 | 0.21–0.51 |
| 5.8 | 0.48 | | 1 | 8 | NA | 3 | 1 | 1 | 0.22–0.53 | 0.21–0.51 |
| 5.9 | 0.49 | | 1 | 8 | NA | 3 | 1 | 1 | 0.21–0.53 | 0.21–0.51 |
| 6 | 0.50 | | 1 | NA | NA | 4 | 1 | 1 | 0.31–0.76 | 0.31–0.75 |
| 6 | 0.50 | | 1 | 10 | NA | 5 | 1 | 1 | 0.49–0.92 | 0.47–0.87 |
| 6 | 0.50 | | 1 | 9 | NA | 6 | 1 | 1 | 0.47–0.91 | 0.42–0.82 |
| 6 | 0.50 | | 1 | 8 | NA | 4 | 1 | 1 | 0.27–0.63 | 0.25–0.59 |
| 11 | 0.92 | | 1 | 9 | NA | 6 | 1 | 1 | 0.46–0.92 | 0.42–0.82 |
| 11 | 0.92 | | 1 | 9 | NA | 8 | 1 | 1 | 0.51–1.07 | 0.46–0.96 |
| 11 | 0.92 | | 1 | 10 | NA | 8 | 1 | 1 | 0.67–1.18 | 0.63–1.05 |
| 11 | 0.92 | * | 1 | 10 | NA | 10 | 3 | 1 | 1.03–1.75 | 0.97–1.45 |
| 11 | 0.92 | | 1 | 10 | NA | 9 | 1 | 1 | 0.69–1.32 | 0.66–1.13 |
| 12 | 1.00 | | 1 | 12 | NA | 9 | 1 | 1 | 0.88–1.60 | 0.80–1.36 |
| 12 | 1.00 | | 1 | 10 | NA | 8 | 1 | 1 | 0.66–1.18 | 0.63–1.05 |
| 12 | 1.00 | | 1 | 10 | NA | 6 | 1 | 1 | 0.59–1.00 | 0.54–0.90 |
| 12 | 1.00 | | 1 | 10 | NA | 8 | 1 | 1 | 0.66–1.19 | 0.63–1.05 |
| 12 | 1.00 | * | 1 | 11 | NA | 9 | 3 | 1 | 1.07–1.60 | 1.01–1.41 |
| 12 | 1.00 | | 1 | 10 | NA | 9 | 3 | 1 | 1.00–1.53 | 0.95–1.37 |
| 12 | 1.00 | | 1 | 10 | NA | 9 | 3 | 1 | 0.99–1.52 | 0.95–1.37 |
| 12 | 1.00 | * | 1 | 11 | NA | 9 | 3 | 1 | 1.06–1.60 | 1.01–1.42 |
| 19.5 | 1.63 | | 2 | 13 | NA | 9 | 5 | 1 | 1.50–2.24 | 1.33–1.81 |
| 19.5 | 1.63 | | 2 | 13 | NA | 9 | 6 | 1 | 1.66–2.39 | 1.49–1.93 |
| 19.5 | 1.63 | | 2 | 13 | NA | 9 | 5 | 1 | 1.50–2.24 | 1.33–1.82 |
| 19.5 | 1.63 | | 2 | 13 | NA | 9 | 5 | 1 | 1.49–2.24 | 1.32–1.82 |
| 19.5 | 1.63 | | 2 | 13 | NA | 9 | 5 | 1 | 1.50–2.23 | 1.33–1.82 |
| 31.5 | 2.63 | | 2 | NA | 6 | 10 | 9 | 5 | 2.70–3.61 | 2.43–3.01 |
| 31.5 | 2.63 | | 2 | NA | 7 | 11 | 9 | 5 | 2.92–3.87 | 2.58–3.19 |
| 31.5 | 2.63 | | 2 | NA | 7 | 10 | 9 | 4 | 2.77–3.59 | 2.49–3.04 |
| 31.5 | 2.63 | | 2 | NA | 6 | 9 | 9 | 3 | 2.34–3.08 | 2.24–2.73 |

*Fig. 3. Comparison of age estimates with ages of known age animals. References: 1 – O'Connor (1998); 2 – Deniz and Payne (1982). NA = not observed. * = discrepancy between estimated and known ages # refer to column 1 of Fig. 1 and read across to find Deniz and Payne (1982) or Rowley-Conwy (1997) equivalents.*

| Stage | Payne (1973) range (years) | Defining state # | Male 95% confidence range | Female 95% confidence range |
|---|---|---|---|---|
| A | 0–0.17 | dp4 < 5 | -0.39–0.11 | -0.39–0.16 |
| B | 0.17–0.5 | dp4 > 4, M1 <3 | 0.01–0.36 | 0.01–0.44 |
| C | 0.5–1 | M1 >2, M2 <3 | 0.33–1.25 | 0.28–1.19 |
| D | 1–2 | M2 >2, M3 <3 | 0.92–2.22 | 1.00–2.49 |
| E | 2–3 | 2 < M3 < 7 | 1.98–3.37 | 2.04–4.27 |
| F | 3–4 | 6 < M3 < 11 | 2.92–4.84 | 3.26–5.86 |
| G | 4–6 | M2 = 9, M3 = 11 | 4.15–6.67 | 4.32–7.28 |
| H | 6–8 | M2 > 9, M3 = 11 | 4.96–8.03 | 5.83–10.52 |
| I | 8–10 | M3 > 11 | 7.22–12.87 | 8.25–12.91 |

*Fig. 4 Estimated ages (in years from birth) for animals in Payne mandible wear stages A–I. # numerical states refer to column 1 of Fig. 1 and read across to find Deniz and Payne (1982) or Rowley-Conwy (1997) equivalents.*

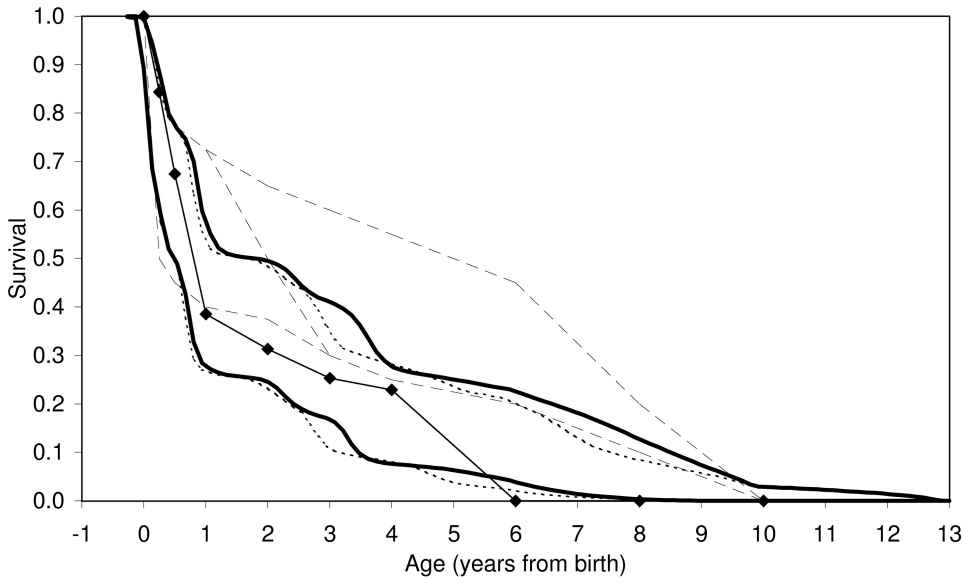



*Fig. 5. Survivorship curves for the Early Neolithic sheep and goats at Arene Candide. Key: Dashed lines: Payne idealised curves as in Fig. 2. Thin solid line with diamonds: Rowley-Conwy's (1997) curve. Solid line: posterior 95% confidence interval if all individuals are female. Dotted line: posterior 95% confidence interval if all individuals are male.*

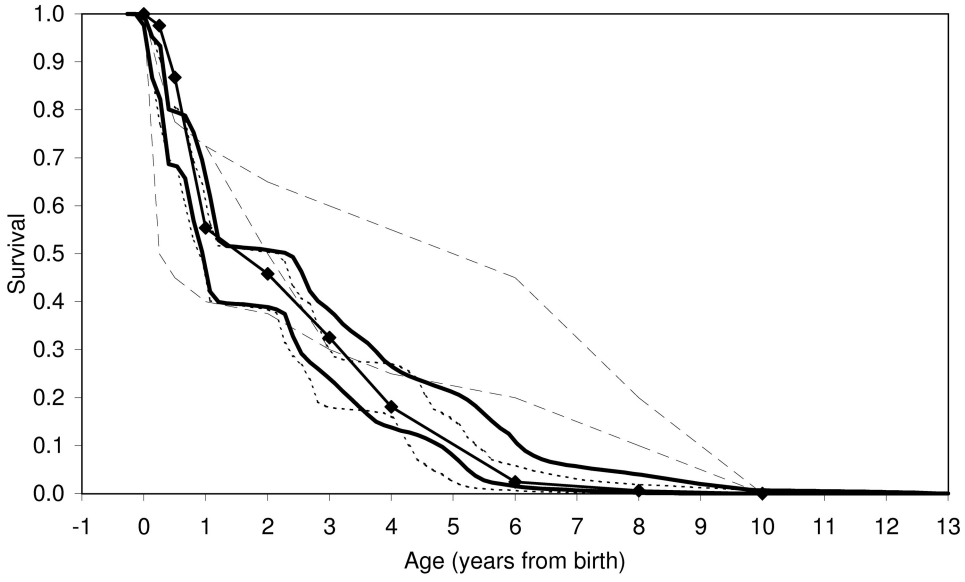



*Fig. 6. Survivorship curves for the Middle Neolithic I sheep and goats at Arene Candide. Key: as Fig. 5.*

with the Arene Candide data, and to Gill Jones for extensive discussion of the issues of ageing sheep from toothwear. Gill Jones and Caitlin Buck provided helpful comments on an earlier draft. Gill Jones also suggested the term "grouped stages". Finally, thanks to Deborah Ruscillo for all her work in organising an excellent conference session and editing this volume.

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*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 155–178*

# 10. Tooth Eruption and Wear Observed in Live Sheep from Butser Hill, the Cotswold Farm Park and Five Farms in the Pentland Hills, UK

*G. G. Jones*

*Following Deniz and Payne's work on goats (1982), 1611 observations of live sheep were made, to provide modern information useful in making age estimates in archaeological studies of husbandry and seasonality. Breeds studied were the Soay, Scottish Blackface, Shetland, White-faced Woodland, other traditional breeds and commercial crossbreds. Details are given of the tagging systems, date of birth, intervals of visits, practical difficulties, accuracy and grouping of stages. Figures show results for incisor eruption, and eruption and wear for dp4, P4 and the molar teeth. Overall results are summarized using Payne's mandible stages, sub-divided using wear on the most recently-erupted tooth. Results from different breeds show a general similarity for all sheep, with Blackfaces similar to the traditional breeds, but some Soays erupting late. Differences between sheep and goats are seen in dp4 wear and the order of eruption of P4 and M3. Relative wear on adjacent teeth is shown as a means of studying wear-rate, and hence adjusting age-estimates for mandible stages which depend on wear. Comparisons of wear-rate show differences between the study sheep, UK Romano-British to medieval sheep and Neolithic Greek sheep.*

## Introduction

The study of dental eruption and patterns of wear in the lower jaw of sheep is well established in zooarchaeology and is used to estimate age at death. This provides important clues concerning husbandry practices. The eruption of incisor teeth is used by farmers to give a general indication of age especially in young sheep, but the cheek teeth, being difficult to see, are not examined and there is little modern information on them. In excavated material it is the cheek teeth which are useful, as the teeth are deeply set within the jaw and survive well in contrast to the incisors, which are usually lost *post mortem*. Estimates of age at death have relied on old data, primarily those quoted by Silver (1969), which were based on Simonds (1854) and Brown (1860), on Payne's work on sheep and goats (1973), and Deniz and Payne's work on goats (1979, 1982). The problems are much discussed in the literature and are summarized by Moran and O'Connor (1994) in their study of dental and epiphysial fusion in aged sheep from museum collections.

Deniz and Payne studied tooth eruption and wear in live Turkish Angora goats, and their method was used in this study of British sheep. Observations were made on 1611 live sheep in three locations and of various breeds, including primitive and traditional. The primary aim was to provide modern information useful to the zooarchaeologist making age at death estimates, and inferring ancient husbandry practices and season of slaughter. Secondarily, information was sought on whether large differences could be seen between the groups of sheep examined, and whether results for these UK sheep were similar to those from the Turkish goats.

## Materials

### *The sheep and farms*

Sheep were examined in three places: at the Cotswold Farm Park (CFP) in Gloucestershire, at Butser Ancient Farm Project in Hampshire, and, via the work of the Animal Diseases Research Association, The Moredun Research Institute, at several hill farms in the Pentland

| Farm | Breed | 0–12 mo 1st year | | 13–24 mo 2nd year | | 27–36 mo 3rd year | | 42–60 mo 4/5th year | | 66–84 mo 6/7th year | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Rec | Ind | Rec | Ind | Rec | Ind | Rec | Ind | Rec | Ind | Rec. | Ind. |
| **Butser Ancient Farm** | Soay | 186 | 48 | 98 | 24 | 66 | 13 | 50 | 9 | 19 | 3 | 419 | 65 |
| 641 observations | Shetland | 46 | 11 | 7 | 2 | | | | | | | 53 | 11 |
| of 107 sheep | Hebridean | 27 | 8 | 18 | 3 | 23 | 4 | 13 | 4 | | | 81 | 14 |
| | Manx Loghtan | 13 | 3 | 6 | 2 | 6 | 2 | 6 | 1 | 3 | 1 | 34 | 6 |
| | Mouflon | 7 | 2 | 7 | 2 | 1 | 1 | 7 | 1 | 2 | 1 | 24 | 4 |
| | Mouflon x Soay | 4 | 1 | 2 | 1 | | | | | | | 6 | 1 |
| | Soay x Suffolk | 17 | 6 | 7 | 2 | | | | | | | 24 | 6 |
| BAF of uncertain age 194 of 27[1] | 14 Soay, 13 others | | | | | | | | | | | | |
| **Cotswold Farm Park** | Whitefaced Woodland | 38 | | 52 | | 27 | | 14 | | 2 | | 133 | 80 |
| 488 observations | Shetland | 24 | | 55 | | 25 | | 19 | | 1 | | 124 | 54 |
| of 337 sheep | Jacob | 16 | | 20 | | | | | | | | 36 | 33 |
| | Other minority breed | 12 | | 14 | | 15 | | 18 | | 9 | | 68 | 62 |
| | commercial cross | 32 | | 38 | | 4 | | 20 | | 33 | | 127 | 108 |
| **Pentlands: hill farms** | Scottish Blackface | 32 | | 41 | | 34 | | 67 | | 45 | | 219 | [2] |
| **Pentlands: lowland** | Scottish Blackface | 18 | | 10 | | 8 | | 32 | | 1 | | 69 | |
| 288 observations | | | | | | | | | | | | | |
| **Total** | | 472 | | 375 | | 209 | | 246 | | 115 | | 1417 | |

Rec. – records; Ind. – individuals; [1] - not included in the main study, but used in the reversals study; [2] – not individually tagged.

*Fig. 1. Number of observations, and number of individual sheep seen, in each year class.*

Hills south of Edinburgh. The breeds seen and number of observations are shown on Fig. 1, a total of 1417 observations of known-age sheep on which this study is based. A further 194 observations of older sheep at Butser were of uncertain age; but these results were useful for studying errors (see below). Nearly all sheep over a year old were ewes (825 records of ewes, 65 of rams, no castrates).

The CFP is on limestone, and the sheep had access to extensive good quality grazing with some winter feeding of hay and concentrates. The breed seen most regularly was the White-faced Woodland, with further records of unimproved coloured Shetlands, Jacobs and commercial crossbreds, plus occasional records of Hebrideans, Welsh Mountains, Orkneys, Herdwicks and Manx Loghtans. Visits were three-monthly. The commercial sheep were mostly second generation crosses, of (Swaledale x Colbred) x Colbred, or Mules (Swaledale x Blue-faced Leicester) x Colbreds.

At Butser, on the chalk South Downs, pasture was sufficient but more restricted. Some sheep were kept for part of the time in the grounds of Fishbourne Roman Palace. Where necessary, winter feed was given as hay with some concentrates. Sheep examined were Soays, and a smaller number of unimproved Shetlands, Manx Loghtans, Hebrideans, four Mouflons and one Mouflon x Soay. Visits were monthly.

Two visits were made to Scotland, joining John Spence's group studying premature incisor loss ('broken mouth'). The sheep, all Scottish Blackfaces, were on hill farms with extensive rough grazing of heather and grass, with extra feed of hay and/or fodder crops in bad conditions in the winter and at lambing time, and with access to low ground fields before the rams are introduced in November. In addition, on two occasions when the weather was too bad for the hill sheep to be brought down, some Blackfaces belonging to the Moredun Institute were seen. These were maintained on low ground pastures with extra feed over the autumn/winter and lambing period in the form of concentrates and roots, and may also have been put in a turnip field. This last area will include high silica/soil uptake.

### *Tagging and date of birth*

At CFP, 360 of the records are from sheep whose age was known to the day. Sheep bore a lambing tag whose first digit represented the year, and usually also a breed registration number tag. Some other sheep (65 records from commercial sheep and 58 from other breeds) were also recorded where their age could with confidence be assigned to one age class; most (72%) were in the age classes which last three or six months. Date of birth could usually by deduced from the lambing tag. Tags were used sequentially, so that a tag of 5101 born on 16/03/85 and a tag of 5113 born on 18/03/85 (both flock book sheep) give a close estimate for tag 5111 (a commercial sheep not written down).

At Butser, day of birth was known for the sheep born during the period of study (1984–87). When a tag was lost, the sheep was retagged with a new number, and the identity could be deduced by elimination plus previous descriptions of colour, etc. Tagging and records were good for some of the Butser pre-1984 born sheep and in a few others, the year of birth was obvious and the age was estimated. Records were made of some older sheep of unknown age and a note of results is made separately.

The Scottish sheep were horn-branded with the year

of birth. Births are mostly between 10th April and 10th May. The two visits of 11–14th September and 19–21 March give estimated ages two or three weeks either side of 4.5 months and nearly 11 months plus the age in years obtained from the horn-brand (0, 1, 2, ...6 years).

The rams ran with the flock all year at Butser, so lambing time followed a natural pattern. In 1985–7, 57 Soays lambs were born between 29th March and 22nd May with a mean birth date of 17th April. These birth-dates are very close to those recorded by Jewell *et al.* (1974) for St. Kilda Soays, where the mean birth date was 15th April (491 sheep observed over three seasons). Thirty-seven other Butser lambs (Shetlands, Manx Loghtans, Hebrideans, the Mouflon and the Mouflon x Soay) were born between 17th March and 24th April with a mean of 8th April. Births at CFP were somewhat earlier, 11th March to 19th April, with an average of 31st March (N 188)(excluding the commercial sheep).

## Method

The method used to record the teeth is described by Deniz and Payne (1982) (and see Plates 1.16 and 1.17 in Davis 1987). The sheep was held by a helper. Records were made of the incisor teeth present, in addition to the wear on the occlusal surface on the left side. The mouth was then held open by placing the speculum (a copy of Payne's original design) in the diastema. A Twinlite torch with fibre-optic, spatula-shaped attachment kept the tongue away from the teeth and provided light in the mouth. The left mandibular teeth were cleaned and recorded with the help of a dental mirror attached to a second Twinlite.

The speculum was used for all the Scottish examinations, the larger breeds from three months, and all breeds (other than Soays) from six months. With the Soays, the smallest breed, a smaller speculum was used. In some cases, the mouth was large enough to use the speculum at five months; at nine months, it could be used in two-thirds of the specimens; it was used in most by eleven months and in all by twenty months.

For young lambs the speculum could not be used and the jaw was held open by placing the left fingers in the diastema. The jaw did not open sufficiently to use the dental mirror, so observations were made directly. This meant that the base of the V between the three elements of the deciduous fourth premolar (dp4) was difficult to see in cases where the cusps in front of the V were still high, thus obscuring the base.

The amount of light in the mouth was variable. On a sunny day, the light behind was a help. On cloudy days working outside, the light given by the torches was less useful than when working in a barn where the eyes were better adjusted to torchlight.

For incisor teeth, both eruption (of both left and right sides) and wear (left only) were recorded but only eruption has been summarized here. The stages used (Figs 8 and 10) show how many permanent incisors were present (right plus left) in usual agricultural practice. In the stage 'two-tooth', both first incisors were at full occlusal height (but not necessarily showing dentine wear). In the 'E/H/ one' stage, the right and/or left side was erupting or half up, or one only was at full height.

The stage 'not yet erupted' means not erupted into the mouth cavity, 'E' means just through the gum line, and 'H' means about halfway between the gum and full height. 'E' and 'H' are therefore more advanced than Ewbank *et al*'s (1964) codes for archaeological specimens. 'J', enamel wear only, is a very brief stage for sheep, and has been joined with 'E' and 'H'. The phrase 'in wear' has been used to mean that dentine has been exposed on the tooth. This practice follows Payne (1973, 293) and is often used for sheep, cattle and deer; note, however, that it should not be extended and applied to pigs, where the enamel is much thicker, and the definition of 'in wear' should begin at the 'enamel wear only' stage. The wear stages (Payne 1973 and 1987) record numerically the four aspects of progressive tooth wear: initial dentine wear on each cusp, the number of dentine joins between cusps, the long-lasting mature wear stage (9A for M1 and M2, 11G for M3, 14L for dp4) and, as the tooth wears to its base, the gradual erasure of the dental infundibula, the 'islands' of enamel.

The visits were made entirely through the generosity of the various organisations, and the specimens examined were what were possible and practicable, which was not always ideal; e.g., at CFP sometimes a particular group were grazing some miles away from the handling pens and were not seen; sometimes it was convenient to see the smaller groups of sheep on display to the public and not the whole group of a breed. The two Scottish visits occurred during the Institute's fieldwork which did not match well the already-established 3, 6, 9 months for visits to CFP. Visits were not made at lambing time but were made a month later. Because date of birth was known, one visit at CFP gave results for more than one month class.

The age classes used were as follows: 0 (birth to 15 days), 1 month (16 days to 1 month, 15 days), 2 months (1 month, 16 days to 2 months, 15 days), and so on up to 22 months. For the third year, three-month classes were used: 24 months (22.5 to 25.5 months), and so on. For older sheep, six-month classes were used: 36 months (34.5 months to 39 months, 0 days), 42 months (39 months, 1 day to 45 months, 0 days), 48 months (45 months, 1 day to 51 months, 0 days), and so on.

The data were recorded in notebooks, and then onto a computer using a Microsoft Access database.

Note, on the tables summarizing results for each tooth, that the distribution in the columns, which shows the range of stages seen in sheep of a particular age, gives more reliable information than the distribution in the rows – the ages at which a particular stage was seen. The latter is the more interesting of course, but it is affected

by differences in sample size, composition (e.g. no CFP sheep of 0, 1, 2, 5, 11 or 12 months were seen) and independence. Results for CFP and Scottish Blackfaces are independent or nearly so, but at Butser, particularly at the later ages, many records are from a few individuals. A simple approach has been taken with the presentation of results, with the sample size directly shown. On Figs 3 to 9, the stage which includes the median value, where half the values are at or before and half or at or beyond this stage, is bold and underscored. The central two-thirds of the columnar distribution approximates to 1 standard deviation. Outlying results are not given undue emphasis in the discussion; the outlying 1 in 20 values approximate to those beyond two SD.

Descriptions of teeth follow Hillson (1986, 11 and 19–20) in the use of 'element' for the pairs of molar cusps, 'infundibulum' for the island of enamel, and lingual/buccal for tongue/cheek side. For sheep cheek teeth, the use of anterior and posterior (towards the front or back of the jaw) is equivalent to mesial and distal. For the third part of M3 (the hypoconulid, Hillson, Fig. 3.1), the 'posterior cusp' (when describing initial wear) or 'element' is used.

### *Mandible stages*

With archaeological samples, it is usual to group the mandibles into stages based on eruption and wear, e.g., Ewbank *et al.* 1964, Higham 1967, Payne 1973, Grant 1975, 1982, Bourdillon and Coy 1980, O'Connor 1991, allowing the data to be shown on a single table or figure. The sheep studied here are summarized using Payne's stages, which do not depend on aspects of development (for example Ewbank's stage 'tooth visible in the crypt') which cannot be seen in the live animal. Because the sample sizes are substantial, and the duration of some of Payne's stages is quite long, the stages were subdivided. In an archaeological sample with, for example, many mandibles at stage C (M1 in wear, M2 not yet in wear), it is of interest to know if most are early within the stage, or late, or well-spread. The study of sheep at the Romano-British temple at Harlow is an example (Legge 1985). By drawing the typical 'A,B,C...I' histogram larger, and using a horizontal line within the stage C bar, the proportion at each M1 tooth wear stage could be shown, grouped according to the appropriate level of detail for the site and sample. The late mandible stage 'I' is renamed as 'J' in this paper, because of its greater legibility ('I', particularly in sans serif fonts, may be confused with the numeral '1').

The subdivision of stages used for the overall summary and the breeds summaries were based on the spread of stages by age observed for each tooth. Stage C was subdivided into C1/2, C3/4, C5 and C6+ using the wear stages of M1. Stage D (M2 in wear, M3 not yet in wear) was similarly divided using the wear stages of M2. Stage E was given two stages, E1/2 and E3+, using the wear on the first element and then the second element of M3. Stage F, where the posterior element of M3 is in wear, is divided into F5/8 and F9/10, using the wear on M3. Stage G has been subdivided on the basis of wear on M1, Ga where M1 is at 9A and Gb where any part of the infundibula of M1 are worn away.

There is a case for making the final subdivision of stage C to be 'M1 in wear, M2 E/J' (erupting, half up or just in enamel wear)(abbreviated to 'Cej'), and similarly for stage D ('Dej'). 'Dej' is the same as O'Connor's 'Subadult 2' (1991). For the study sheep, it was decided that the quality of data for C5 and C6+ was better than for E/J (more easily seen in the live animal), and there is a difference of meaning for 'E' between live sheep and archaeological specimens. There is an archive version of Fig. 9, using C5+ and Cej as the final subdivisions for C, or results can be calculated using Figs 9 and 5 (plus Fig. 6 for calculating D5+ and Dej).

## Results

### *Stages used, and grouping of stages*

Recording of the teeth present, the initial, the mature wear and the late wear stages proved on the whole reliable (see Accuracy, below), but the intermediate stages where dentine becomes gradually continuous between cusps were more difficult. The length of time that the head of the sheep was stationary was usually short and always the first few seconds were taken with identifying which cusp belonged to which tooth. Determining whether the dentine exposed on a tooth is continuous between cusps is a procedure normally done on dry archaeological material with a hand lens. Although the spatula-shaped Twinlite kept the tongue away from the teeth, and the second mirror kept the cheek away from the teeth, saliva produced by the papillae (see Weinreb and Sharav 1964, Fig. 7) was a problem. Drying with a cloth was tried, but moisture returned very quickly.

Many of the records could be given only to a range of stages. For example, many were recorded as either 4A or 5A, and in these the dentine was nearly, or just, continuous at the anterior edge, i.e. they were late within stage 4A or early within stage 5A. The grouped stages were frequent for the third molar, even to three or four stages. These grouped stages are safely within the second major stage between initial wear and the mature-wear stage. They were not, therefore, excluded, which would have altered the calculation of the median value. The grouped-stage records are sometimes numerous and show a spread of age classes as expected, see 8A and 8/9A for M2, 84 and 74 records respectively. Levitan (1982, Fig. 4, 213) shows the difficulty clearly. A few grouped results for P4 were excluded (see Fig. 7).

For the deciduous fourth premolar, dp4 the many stages between initial wear on all six cusps, 6L, and the

| | | **dp4** | | **P4** | | **M1** | **M2** | | **M3** |
|---|---|---|---|---|---|---|---|---|---|
| No. of observations | | 408 | | 365 | | 773 | 635 | | 409 |
| No. of reversals | | 16 | | 28 | | 19 | 24 | | 22 |
| Percentage of reversals | | *3.9%* | | *7.7%* | | *2.4%* | *3.8%* | | *5.4%* |
| Early wear stages | nye to 6L | 0 | nye to 2A | 0 | nye to 4A | 2 | 1 | nye to 4A | 5 |
| Intermediate wear stages | 6L to 14L | 0 | 2A to 12S | 21 | 5A to 9A | 9 | 22 | 5A to 11G | 17 |
| Late wear stages | 14L to 22L | 16 | 12S to 15A | 7 | 9A to 15A | 8 | 1 | | |
| Adjacent stages | | 7 | | 12 | | 9 | 16 | | 8 |
| Two stages apart | | 7 | | 5 | | 5 | 6 | | 10 |
| More than two apart | | 2 | | 11 | | 5 | 2 | | 4 |
| Average interval between observations with reversal | | 2.25 mo | | 3.17 mo | | 3.70 | 2.90 | | 2.46 mo |

These include the older Butser sheep of uncertain age seen more than once. nye – not yet erupted.

*Fig. 2. Reversals in 773 observations of 105 Butser sheep seen more than once.*

mature wear stage, 14L (6 cusps in wear + 8 dentine joins = 14), were grouped into fewer stages. For example, the stage 7/10K (6 cusps + 1 to 4 joins), with two dots shown between the first and second pair of cusps, includes records where dentine was partly continuous at this point (e.g. 8L). It also included records where there was uncertainty: to quote a field note 'they're quite close to through, but the dentine narrows so that I can't be sure'. A more detailed study of the stages observed could be done from the archive record. The erasure of the anterior infundibulum of dp4 is gradual, and is defined as 16L when 'the length of the island (including the enamel) is less than 50% of the length of the lobe' (Payne 1973, 289). An intermediate stage, 15K, was added for cases where the anterior element was already wearing flat and the infundibulum was reduced in size, but before 16L.

Similarly, for P4 a stage 13S was added, between 12S and 14S. 13S should be included with 12S for comparison with archaeological records. A stage 5/12W was used for records where the anterior infundibulum was isolated, but the wear on the posterior part of the tooth was uncertain.

For molar teeth, the stages 6A/7A (7G/8G for M3s with the posterior cusp in wear) was combined throughout. This stage change depends on seeing clearly the bottom of the V-shape at the central part of the tooth, whereas for distinguishing 5A from 6/7A, 6/7A from 8A and 8A from 9A, the dentine join is at the lingual edge of the tooth and is easier to see.

Stages 1A and 2A were combined for simplicity, as were 3A and 4A. Neither 1A nor 3A were common. Cases of 1A and 1/2A (uncertain whether 1A or 2A) were 4 and 1 for M1, 2 and 0 for M2 and 10 and 4 for M3. Cases of 3A and 3/4A were 4 and 0 for M1, 8 and 0 for M2 and 7 and 2 for M3.

Within the six months of the later age classes, individual Butser sheep were seen several times, and a tooth may have passed through two or more stages, or it may have remained at one stage giving several records. (Theoretically this could be as many as six, but a maximum of four was used).

The results for Scottish Blackfaces at 4.5 months were allotted randomly to the adjacent age classes 4 and 5 months, half each, and, similarly, the 10.75 months to 10 and 11, quarter/three-quarters each, and so on for later age classes. They are shown separately, however, on Figs 11 and 12 in the Appendix below.

### *Accuracy*

At Butser, 78 sheep of known age were seen more than once (579 records), and the development of individual sheep could be followed. A further 194 observations of 27 older sheep of uncertain age were recorded at Butser, and these are included here as they give information about later stages, making a total of 773 observations of 105 sheep.

This provided a useful check on accuracy. For example, if a sheep was recorded as showing an earlier stage than that recorded previously, the apparent 'reversal' indicated an error. Reversals are summarized on Fig. 2. They were fewest for M1 and increased, as would be expected, for the more distant M2 and then M3. Reversals for dp4 were all at later wear stages and indicate some inaccuracy in describing the erasure of the infundibula. Reversals were high for P4 and cast doubt on the validity of the P4 records as a whole. The tooth is of a more irregular shape than either dp4 or the molars, and frequently the posterior part of the tooth was difficult to define. In particular, in sheep of the age where dp4 is replaced and P4 comes into full wear, the primary focus of attention was the eruption and wear of the molars, and probably less time was spent on dp4/P4.

Most reversals were between adjacent stages, using Payne's numerical coding, e.g. 9A recorded and 8A on a subsequent visit, or two stages away, e.g. 8G to 6G in M3. The average interval between observations where there was a reversal was 2.25 to 3.70 months. The overall proportion of reversals was 4.21%.

Reversals were used unchanged in the summaries, except in the following two situations, where the record was treated as 'no data'. Firstly, in a few cases the reversal

followed three or more previous observations of the later stage. Secondly, in five records, reversals suggested that a tooth was wrongly identified. In one case, for example, three consecutive records give: dp4 15K, 16L and 18P; M1 9A, 8A and 9A; M2 5A, 5A and 6/7A; and M3 2A, not yet erupted and 3C/5A. That is, it is likely that the middle of these three records has mistaken the posterior pair of cusps present as the posterior part of M2 rather than the anterior part of M3.

Reversals were only slightly higher for Soays, than for Butser other breeds, despite the narrower speculum gap (4.42% for all four cheek teeth, and 4.01%, respectively).

There is a greater likelihood of error with the sheep records than with Payne's goat records, where there was only one reversal for cheek teeth in 367 observations of goats seen more than once (although far fewer goats were seen repeatedly than here). The goats studied had long horns, so that it was possible to hold the animals still. The sheep studied were mostly without horns. It was hoped that the horned breeds (Blackfaces in Scotland and White-faced Woodlands at CFP) would be a little easier to hold, but their horns were not long enough to exert much leverage. The ease of holding depended rather on body weight, so that the smaller breeds were in this respect easier, and in practice the White-faced Woodlands were large and very strong. Quite often the Soays would just give up and stand still. The speculum gap used for the sheep was smaller than that used for the goats. In the goat kids, the speculum could be used in all cases.

### *First year*

During the first year, the increase in stage with age (Figs 3 and 4) can be seen, with the median value showing a regular pattern. For dp4 and M1 in three-quarters of the age classes, half or more records were at a single stage. After the first few months the span of ages at which a stage was observed increased, often to several months.

In six day-old lambs and one 5-day old, all three deciduous premolars could be clearly felt though they were still under the gingival membrane, which was very thin. Dp4 was a little higher than dp2 and dp3 but all were certainly above the alveolar bone, and might score 'half up' or 'up and unworn' in an archaeological specimen. In another day-old and two five days old lambs, the middle pair of dp4 cusps were through the gum, and in a lamb 'about six days old' all dp4 cusps were through but unworn.

At age class '1 month' (16 days – 1 month, 15 days), dp4 was unworn or at early wear stages, and by two months (1 month, 16 days – 2 months, 15 days) all dp4's observed were in wear, with most showing wear on all six cusps, 6L. By three months all had reached 7L and many were at later stages. At four and five months, the stages where dentine gradually becomes continuous between cusps predominated. By six months the anterior infundibulum was isolated in all cases (with one possible exception, at 7/13K), and the mature wear stage 14L was the commonest stage observed; this continued at seven and eight months. At nine months, not many cases were pre-14L and already a few showed some erasure of the anterior infundibulum.

In Fig. 15 in the Appendix, the wear stages of dp4 are shown against those of M1. At M1 stage E/J, most dp4 records were at 7L. Higher wear scores for dp4 may indicate fast wear, or the presence of goat, particularly if other characteristics of goat are present (Payne 1985), see below under 'Relative wear and Sheep/goats'.

Eruption of the first molar was seen to occur over a very short time, with none in wear at two months, a large group erupted or in enamel-wear, and many already in wear, at three months (2 months, 16 days – 3 months, 15 days) and most at wear stage 1/2A at four months. The few cases of M1 not yet in wear at four and five months were all Soays (see Fig. 11 in the Appendix). Stage 1/2A was observed in a third of the results at three months and more than half the results at four and five months. The later stage 3/4A, where the posterior element of M1 comes into wear, included more than half the results at six and seven months. This notable difference between 1/2A and 3/4A is the basis for dividing the mandible wear stage C into C1/2 and C3/4, used in the overall summaries. Results suggest that it takes a little over two months for M1 to move from initial wear to wear on all cusps, i.e., stage 4A.

Joining of the dentine at the anterior edge of the tooth (5A) was common from six to nine months, and at eight months the median value was at 5A. Note that at eight months, there was a spread of stages observed from 4A to 6/7A. At nine and ten months, more than half of records were at 6/7A. 9A was reached in a very few cases before twelve months.

Eruption and wear of the second molar is shown on Fig. 5. M2 was erupted but not in wear (E/J) in less than half of cases observed at nine months and more than half at ten months. At both 10 and 11 months the median value was at E/J, i.e. at ten and eleven months less than half had reached Payne's mandible stage D, M2 in wear. In the 11 months group of Blackfaces, half were in wear. No CFP sheep were seen at 11 or 12 months because of lambing time. By 13 months 1/2A was the most frequent stage and with almost as many at 3/4A. It is a reasonable deduction that at 12 months the median value would have fallen at 1/2A, with a reasonable number still at E/J, had more sheep been seen. Eruption for M2 was given as 9-12 months by Silver (1969). The coming into wear, the beginning of Payne's Stage D, can be given as 10–13 months, from this study. Eruption into the mouth cavity had occurred during the winter and the tooth was in occlusion, ready for the new grass of spring.

The stage E/J, 'erupted but not in wear' was frequent over the four age classes 9 to (presumed) 12 months (8 months, 16 days – 12 months, 15 days), which is much longer than for M1 where only at 3 months was it frequent.

| Dp4 Stages | Years Months | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 1 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 2 24 | 27 | 30 | 33 | 3 36 | 42 | 48 | 54 | 4 60 | 66 | 72 | 78 | 5 84 | 6 | 7 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| nye/U/J | | **12** | 12 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 24 |
| 2-4 | | | **18** | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 20 |
| 6L | | | 2 | **15** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 17 |
| 7L | | | 4 | 9 | **25** | 4 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 42 |
| 7/10K | | | | | **10** | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 12 |
| 7/13K | | | | | 7 | **16** | 13 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 37 |
| 10N | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| 10/13K | | | | | 2 | 9 | **15** | 10 | 9 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 46 |
| 13L | | | | | 3 | 5 | 3 | 4 | 7 | 5 | 1 | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 29 |
| 10/14K | | | | | | 1 | 5 | 5 | **8** | 6 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 26 |
| 13/14L | | | | | | | 3 | 7 | 2 | **7** | 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 24 |
| 14L | | | | | | 1 | 2 | **30** | 13 | **18** | **28** | **26** | **23** | 2 | **31** | **23** | 7 | 14 | 13 | 5 | 10 | 1 | 3 | 1 | | 1 | | 1 | | | | | | | | | | | | 253 |
| 15K 'going' | | | | | | | | | | | 2 | 9 | 4 | | 6 | 9 | 1 | **7** | **3** | 1 | **5** | 2 | 2 | | | 1 | | | | | | | | | | | | | | 52 |
| 16L | | | | | | | | | 1 | | | 4 | 5 | 2 | 16 | 6 | **5** | 11 | 6 | **11** | 7 | **4** | **10** | 6 | 2 | | 1 | | | | | | | | | | | | | 97 |
| 17 1 or ½+½ er. | | | | | | | | | | | 1 | | 5 | | 5 | | 3 | 5 | 3 | 3 | 2 | | **4** | 5 | 3 | 2 | | 1 | | | | | | | | | | | | 42 |
| 18/19 1+ or 1½ er. | | | | | | | | | | | | | 2 | | | | 1 | 1 | 3 | | | 2 | 3 | 4 | 3 | 5 | 1 | 1 | | | | | | | | | | | | 26 |
| 20 2 erased | | | | | | | | | | | | | 2 | | 1 | | 1 | 1 | 2 | 3 | 1 | | 4 | 1 | 6 | | | | | | | | | | | | | | | 22 |
| 21/23 2+ to 3 er. | | | | | | | | | | | | | | | | 1 | | | 1 | | 2 | | 1 | **3** | 6 | 1 | 2 | | | | | | | | | | | | | 17 |
| shed and P4 nye | | | | | | | | | | | | | | | | | | | | | 1 | | 2 | 1 | 2 | 1 | | | | | | | | | | | | | | 7 |
| **P4** E/H | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | 6 | **13** | 4 | 4 | 3 | | | | | | | | | | | | 32 |
| P4 U/J | | | | | | | | | | | | | | | | | | | | | | | | 3 | 7 | **9** | 7 | | | | | | | | | | | | | 26 |
| P4 in wear | | | | | | | | | | | | | | | | | | | | | | | | 5 | 3 | 21 | **38** | **36** | 51 | 87 | 40 | 67 | 35 | 47 | 23 | 26 | 3 | | | 482 |
| P4 shed | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | 3 | 2 | | | | 8 |
| Total | | 12 | 36 | 26 | 50 | 38 | 41 | 57 | 40 | 36 | 39 | 39 | 41 | 4 | 60 | 39 | 18 | 39 | 31 | 23 | 28 | 10 | 30 | 35 | 45 | 45 | 53 | 42 | 51 | 87 | 40 | 67 | 35 | 49 | 24 | 29 | 5 | | | 1344 |

Except where shown, the tables combine results from all sheep; nye – not yet erupted; U/J – all stages from unworn to just enamel wear; wear stages are defined in Payne 1973 and 1987, with additional stages suffixed K described under Method; er. – erased.

*Fig. 3. Dp4 eruption and wear stages, and P4 eruption, by age class.*

| M1 Stages | Years Months | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 1 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 2 24 | 27 | 30 | 33 | 3 36 | 42 | 48 | 54 | 4 60 | 66 | 72 | 78 | 5 84 | 6 | 7 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| nye | | **12** | **35** | **22** | 6 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 77 |
| E/J | | | | 3 | **28** | 3 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 35 |
| 1/2A | | | | | 17 | **29** | **27** | 3 | 4 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 80 |
| 3/4A | | | | | | 4 | 10 | **30** | **24** | 4 | 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 75 |
| 4/5A | | | | | | | 1 | 14 | 8 | 11 | 2 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 38 |
| 5A | | | | | | | 1 | 11 | 2 | **7** | 8 | 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 34 |
| 5/7A | | | | | | | | | | 5 | **7** | 9 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 21 |
| 6/7A | / | | | | | | | | 1 | 9 | 19 | **19** | 18 | | 1 | | | 2 | 2 | | | | | | | | | | | | | | | | | | | | | | 71 |
| 6/8A | | | | | | | | | | | | 1 | **9** | | 6 | | | | | | | | 1 | | | | | | | | | | | | | | | | | | 17 |
| 8A | | | | | | | | | | | | | 6 | **3** | **31** | 15 | **11** | 16 | **15** | 8 | 5 | 4 | 13 | 9 | 3 | 6 | 1 | 1 | | | | | | | | | | | | | 147 |
| 8/9A | | | | | | | | | | | | | 4 | 1 | 10 | **15** | 5 | **8** | 10 | 2 | 8 | | **4** | 1 | | | | 1 | | | | 1 | | | | | | | | 70 |
| 9A | | | | | | | | | | | | 1 | 3 | | 13 | 9 | 3 | 13 | 5 | **11** | **14** | **7** | 13 | **23** | **42** | **38** | **47** | **43** | **53** | **85** | **37** | **45** | 18 | **26** | 5 | 7 | 1 | | | 562 |
| 10A/B | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | 1 | 3 | | | | 7 |
| 11A/B | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 2 | 1 | **2** | 2 | | | | | | | | 8 |
| 12A | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 3 | 15 | 13 | 16 | **6** | **10** | **2** | | | | | 66 |
| 13A | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 |
| 14A | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | 2 | **1** | 1 | | | | | | 5 |
| 15A | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 4 | 3 | 8 | 6 | **2** | | | | | 25 |
| shed | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 3 | | 1 | | | | | 6 |
| Total | | 12 | 35 | 25 | 51 | 38 | 40 | 58 | 39 | 36 | 39 | 37 | 40 | 4 | 61 | 39 | 19 | 39 | 32 | 21 | 27 | 11 | 31 | 33 | 45 | 44 | 48 | 45 | 53 | 87 | 43 | 67 | 37 | 51 | 24 | 28 | 6 | | | 1345 |

Stages are defined by the codes, with the diagrams shown at the main stages as an *aide-memoire*.

*Fig. 4. M1 eruption and wear stages by age class.*

No incisor replacement was seen before 13 months, although in a few individuals, the deciduous incisor was shed at 11 months (Fig. 8).

### *Second year*

During the second year, the span of tooth wear stages seen in each age class is greater, and the spread of ages at which a given stage was observed is great, but there are several age classes where the majority of values are at

| M2 Stages | Years Months | 0-6 | 7 | 8 | 9 | 10 | 11 | 1 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 2 24 | 27 | 30 | 33 | 3 36 | 42 | 4 48 | 54 | 5 60 | 66 | 6 72 | 78 | 7 84 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| nye | | 263 | 41 | **35** | **28** | 14 | 6 | | | | | | | | | | | | | | | | | | | | | | | | | 387 |
| E/J | | | | 2 | 12 | **17** | **19** | | 6 | | | | | | | | | | | | | | | | | | | | | | | 56 |
| 1/2A | | | | 1 | | 6 | 12 | 2 | **26** | 4 | | | | | | | | | | | | | | | | | | | | | | 51 |
| 3/4A | | | | | | 1 | 3 | 2 | 22 | 14 | **10** | 13 | 12 | 3 | 2 | 1 | | 1 | | | | | | | | | | | | | | 84 |
| 4/5A | | | | | | | 1 | | 3 | **16** | 4 | **8** | **7** | 2 | | | 1 | 1 | | 1 | | | | | | | | | | | | 44 |
| 5A | | | | | | | | | 3 | 3 | 2 | 9 | 6 | **9** | 7 | 4 | 1 | 2 | 1 | 1 | | | | | | | | | | | | 48 |
| 5/7A | | | | | | | | | 1 | | | 5 | 4 | 1 | **5** | **3** | 1 | 1 | 3 | 4 | 1 | | | | | | | | | | | 29 |
| 6/7A | / | | | | | | | | | 2 | 1 | 4 | 3 | 7 | 12 | 3 | **21** | **16** | **21** | 11 | 10 | 8 | 4 | 3 | | 1 | | | | | | 127 |
| 6/8A | | | | | | | | | | | | | | | | | 1 | 3 | 3 | 2 | 2 | 3 | 2 | 1 | | | | | | | | 17 |
| 8A | | | | | | | | | | | | | | 1 | | | 1 | 6 | 8 | **9** | **15** | **11** | 14 | 16 | 2 | 1 | | | | | | 84 |
| 8/9A | | | | | | | | | | | | | | | | | | 1 | 6 | 7 | 5 | **11** | **13** | **20** | 6 | 1 | | | | | | 70 |
| 9A | | | | | | | | | | | | | | | | | 1 | | | 6 | 14 | 11 | 16 | 39 | **34** | **63** | **35** | **50** | **21** | **28** | **4** | 322 |
| 12A | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | 2 |
| 15A | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 |
| Total | | 263 | 41 | 38 | 40 | 38 | 41 | 4 | 61 | 39 | 17 | 39 | 32 | 23 | 26 | 11 | 27 | 31 | 42 | 41 | 47 | 44 | 49 | 79 | 42 | 66 | 35 | 50 | 22 | 29 | 5 | 1322 |

*Fig. 5. M2 eruption and wear stages by age class.*

a single stage. The span of ages for stage E/J increased from four months for M2 to six months for M3. The span for wear stages was greater, but not always by very much. The mature wear stages (14L for dp4 and 9A for M1), where crown height is gradually reduced without change to the pattern of dentine and enamel seen at the occlusal surface, is obviously long-lasting, but the pattern 'some have reached it', 'more than half have', 'the most frequent stage', 'more than half are beyond', is regular and progressive.

For dp4, more than half the records were at stage 14L from 9 until 14 months. The stage 15K 'going' (defined in 'Stages used', above) should be regarded as within 14L, for comparison with archaeological results using Payne's stages. From 15 to 19 months the median value varied between 15K and 16L. From 20 months on, more than half showed some erasure of the infundibula. Erasure of half or one infundibulum was common, but of two or more was unusual. At 22 months, some replacement of the deciduous tooth by the permanent fourth premolar was beginning, with a few cases of P4 already in wear.

For M1 during the second year, stages before 8A were unusual. 8A was the most common stage until 17 months although stage 9A was already quite frequent by 13 months. Only by the end of the second year was 9A nearly universal. The posterior fold separating the distal pair of cusps reaches quite deeply into the tooth, so that quite a lot of crown height is lost before 9A is reached. (No information is known to the author about the variability in the depth of this fold).

For M2 the age-spread for early wear stages, as with eruption (noted above), was much longer than for M1 at similar stages. Wear on the anterior cusps only (1/2A) was common from 10 to 13 months with a few earlier and later. Stage 3/4A was common from 13 (and probably from 12 months, see above) to 17 months. From 14 to 19 months the stages 4A to 6/7A predominate. At 21 to 27 months the most frequent record was stage 6/7A. Towards the end of the second year, stages beyond 6/7A occurred but were unusual (some Blackfaces at 23 months).

First signs of third molar eruption were seen at 18 months, with a few in wear at 19 and 20 months. At 21 months, more than half were erupted and by 22 months more than half were in wear. As with the second molar, the eruption of M3 appears to be linked to the seasons, the tooth being in occlusion by the spring, that is, at the beginning of the animal's third year.

For most breeds, the first incisors erupted and came into occlusion at 13 to 16 months (Fig. 8). Most of the later records are Soays and Mouflon (including 9 of the 11 at 17 months with di1 still present). Considering all breeds together, at 21 and 22 months there were a few cases of the permanent first incisor still unerupted, and a few with some eruption of the second incisor. This is a much greater variation than seen in molar eruption.

### *Sheep aged two to seven years old*

Note the change in scale at 24 months, at first showing 3 months, then six months age classes (defined under Method). The spread of time over which each stage was observed continued to increase, as expected, but the pattern of gradual increase of stage with age continues.

At two to four years old, the first molar was, with few exceptions, at the mature wear stage of 9A. By 4.5 years, a third were at later stages, and at 5 and 5.5, about half were at later stages. Although 9A was observed even up to 7 years old, from 6 years old more than half of records showed some erasure of the infundibula. This stage, M1 beyond 9A, is used to divide the mandible stage G in the overall summary. Although it is a poor indicator of age in comparison with eruption and early wear stages, the proportion at Gb is greater with increasing age. There were a few cases where M1 was beyond 9A before M3 reached 11G (five, all four years or older; plus nine possible cases: one where M3 was 9/11G and eight where

| M3 Years | 1¼ | | | | | | | | | 2 | | | | 3 | | | | 4 | | | 5 | | 6 | | 7 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stage Months | 0-14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 24 | 27 | 30 | 33 | 36 | 42 | 48 | 54 | 60 | 66 | 72 | 78 | 84 | | | | |
| nye | 567 | 19 | 39 | **31** | **20** | **20** | **7** | 11 | 8 | 5 | 4 | 1 | | | | | | | | | | | | | | 732 |
| E/J | | | | | 3 | 5 | | **10** | 5 | 8 | 1 | | | | | | | | | | | | | | | 32 |
| 1/2A | | | | 1 | | 3 | 4 | 8 | **13** | **24** | 15 | 10 | 5 | 2 | | | | | | | | | | | | 85 |
| 3/4A | | | | | | | | 2 | 5 | 6 | **12** | **16** | 11 | 8 | 1 | | | | | | | | | | | 61 |
| 4/5A | | | | | | | | | 1 | | 3 | 1 | 4 | 5 | 1 | | 1 | | | | | | | | | 16 |
| 5A | | | | | | | | | 2 | | 3 | 4 | **7** | 2 | 2 | | | | | | | | | | | 20 |
| 4A/7A | | | | | | | | | | | 1 | 2 | | 1 | 2 | | 1 | | | | | | | | | 7 |
| 4A/7G | | | | | | | | | | | 1 | | | 2 | 3 | 1 | | | | | | | | | | 7 |
| 5G/6G | | | | | | | | | | | | 1 | 3 | 1 | 2 | | | | | | | | | | | 7 |
| 6G | | | | | | | | | | | 1 | 3 | 3 | **5** | 9 | 1 | | | | | | | | | | 22 |
| 6G/8G | | | | | | | | | | 1 | | 5 | 5 | 5 | 16 | 2 | 4 | | 1 | | | | | | | 39 |
| 7/8G / | | | | | | | | | | | | 3 | 2 | 16 | **16** | 12 | 1 | 1 | | | | | | | | 51 |
| 7G/9G | | | | | | | | | | | | | 1 | 1 | 8 | 2 | 3 | | | | | | | | | 15 |
| 7G/10G | | | | | | | | | | | | | 2 | 1 | 7 | 2 | 3 | 1 | | | | | | | | 16 |
| 9G | | | | | | | | | | | | | | | 3 | **8** | 2 | 2 | 3 | 1 | | | | | | 19 |
| 9/10G | | | | | | | | | | | | | | | 1 | 1 | 1 | 1 | | | | | | | | 4 |
| 10G | | | | | | | | | | | | | | 1 | 3 | 2 | 2 | 1 | | | | | | | | 9 |
| 9G/11G | | | | | | | | | | | | | 1 | | 5 | 5 | 2 | 3 | 1 | | | | | | | 17 |
| 10/11G | | | | | | | | | | | | | | | 4 | 1 | **15** | 6 | 3 | | | | | | | 29 |
| 11G | | | | | | | | | | | | | | | 3 | 5 | 32 | **21** | **43** | **20** | **29** | **6** | | | | 159 |
| Total | 567 | 19 | 39 | 32 | 23 | 28 | 11 | 31 | 34 | 44 | 41 | 46 | 44 | 50 | 86 | 42 | 67 | 36 | 51 | 21 | 29 | 6 | | | | 1347 |

*Fig. 6. M3 eruption and wear stages by age class.*

| Stage | Years Months | 1¼ 0-14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 2 24 | 27 | 30 | 33 | 3 36 | 42 | 48 | 54 | 4 60 | 66 | 72 | 78 | 84 | 5 | 6 | 7 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| dp4 nye/U/J | | 24 | | | | | | | | | | | | | | | | | | | | | | | | | 24 |
| dp4 in wear | | 534 | 18 | 39 | 31 | 23 | **26** | **9** | **27** | **20** | 20 | 10 | 5 | 3 | | | | | | | | | | | | | 765 |
| dp4 shed,P4 nye | | | | | | | 1 | | 2 | 1 | 2 | 1 | | | | | | | | | | | | | | | 7 |
| **P4** E/H | | | | | | | | 1 | 1 | 6 | **13** | 4 | 4 | 3 | | | | | | | | | | | | | 32 |
| U/J | | | | | | | | | | 3 | 7 | **9** | 7 | | | | | | | | | | | | | | 26 |
| 2A | | | | | | | | | | 4 | 3 | 16 | **22** | 10 | 7 | 1 | 1 | 3 | 2 | | | | | | | | 69 |
| 2A/4A | | | | | | | | | | 1 | | | 3 | 3 | | 3 | | | | | | | | | | | | 10 |
| 4A | | | | | | | | | | | | | 3 | | 1 | 1 | | | | | | | | | | | 5 |
| 7S | | | | | | | | | | | | 4 | 5 | **12** | **22** | 24 | 4 | 4 | | | | | | | | | 75 |
| 8A | | | | | | | | | | | | | 1 | 4 | 6 | **26** | 10 | 5 | 2 | 2 | | | | | | | 56 |
| 8A/9A | | | | | | | | | | | | | 1 | 1 | 1 | 2 | **2** | 1 | | | | | | | | | 8 |
| 5/12W | | | | | | | | | | | | | 2 | 1 | 3 | 9 | **4** | 7 | 2 | 1 | | 1 | | | | | 30 |
| 9A | | | | | | | | | | | | | | 2 | 3 | 2 | **2** | 2 | | | 1 | 1 | | | | | 13 |
| 12S | | | | | | | | | | | | | | 3 | 5 | 15 | 16 | **42** | **22** | **29** | 9 | **16** | 2 | | | | 159 |
| 13S going | | | | | | | | | | | | | | | | | | 1 | 1 | 3 | **5** | 2 | | | | | 12 |
| 14S | | | | | | | | | | | | | | | | | | 1 | 5 | 10 | 6 | 6 | 1 | | | | 29 |
| 15A | | | | | | | | | | | | | | | | | | | | 1 | 2 | | | | | | 3 |
| shed | | | | | | | | | | | | | | | | | | | | 2 | 1 | 3 | 2 | | | | 8 |
| Total | | 558 | 18 | 39 | 31 | 23 | 27 | 10 | 30 | 35 | 45 | 44 | 53 | 42 | 48 | 83 | 39 | 66 | 34 | 48 | 24 | 29 | 5 | | | | 1331 |

Stage 5/12W – anterior infundibulum isolated, posterior part uncertain. (Four records at 4A/7A, 5 at 7S/8A and 4 at 9A/12S are not shown.).

*Fig. 7. P4 eruption and wear stages, and grouped dp4 stages, by age class.*

M3 was at 10/11G; see later discussion of relative wear and archaeological examples).

For the second molar, the change from 6/7A to 9A occurred during the third and fourth year. At 27 to 33 months the median value was the 'open back' stage 8A (all dentine joins complete except for the posterior lingual fold). By three and 3.5 years, half had reached 9A. By 4 nearly all were at 9A with none at earlier stages at 5 years or more. Only three cases of sheep showing later stages were seen, one each at 6, 6.5 and 7 years (and see note on unaged sheep, below).

The third molar results are complicated by many observations which could only be given to a range of stages, reflecting the practical difficulties of seeing into the back of the jaw. However, a broad picture similar to the earlier-erupting teeth can be seen with increasing stage with age. Note that the number of reversals was greater for the third than for the first and second molars

| **Incisors Years** | | | | **1** | | | | | | | | | | | | **2** | | | | **3** | | **4** | | **5** | | **6** | | **7** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Stage Months** | **0** | **1-10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **24** | **27** | **30** | **33** | **36** | **42** | **48** | **54** | **60** | **66** | **72** | **78** | **84** | |
| deciduous nye | **6** | | | | | | | | | | | | | | | | | | | | | | | | | | | 6 |
| **di1 present** | **6** | **412** | **37** | **4** | **57** | **22** | **13** | 4 | 11 | 5 | 3 | | | | | | | | | | | | | | | | | 574 |
| di1 shed, I1 nye | | | 4 | | | | | | | 1 | | 1 | 1 | | | | | | | | | | | | | | | 7 |
| I1 E/H/one | | | | | 6 | 9 | 2 | 1 | 2 | 2 | 4 | 3 | 1 | 2 | | | | | | | | | | | | | | 32 |
| **two-tooth** | | | | | | 11 | 5 | **35** | **20** | **15** | **21** | **7** | **27** | **18** | **24** | 11 | 8 | 2 | | | | | | | | | | 204 |
| I2 E/H/one | | | | | | | | | | | | | 1 | 12 | 11 | 6 | 8 | 4 | 1 | | | | | | | | | 43 |
| **four-tooth** | | | | | | | | | | | | | 2 | 3 | 9 | **24** | **27** | **23** | 9 | 9 | | | | | | | | 106 |
| I3 E/H/one | | | | | | | | | | | | | | | 1 | 6 | 9 | 8 | 4 | 13 | 2 | | | | | | | 43 |
| **six tooth** | | | | | | | | | | | | | | | 1 | 1 | 6 | 9 | **32** | **22** | 17 | 9 | 4 | | 2 | | | 103 |
| six, b.m. | | | | | | | | | | | | | | | | | | | | | 1 | 4 | 2 | 2 | | | | 9 |
| I4 E/H/one | | | | | | | | | | | | | | | | | | 1 | 4 | 22 | **7** | 12 | | 3 | 1 | | | 50 |
| **full mouth** | | | | | | | | | | | | | | | | | 1 | 1 | 2 | 19 | 16 | **36** | **23** | **26** | **13** | **13** | 3 | 153 |
| six/full b.m | | | | | | | | | | | | | | | | | | | | | 1 | 2 | 2 | 1 | | | | 6 |
| full, b.m. | | | | | | | | | | | | | | | | | | | | | 1 | 6 | 8 | 7 | 8 | 15 | **4** | 49 |
| Total | 12 | 412 | 41 | 4 | 63 | 42 | 20 | 40 | 33 | 23 | 28 | 11 | 32 | 35 | 46 | 48 | 59 | 48 | 52 | 85 | 45 | 69 | 39 | 39 | 24 | 28 | 7 | 1385 |

nye – not yet erupted; di – deciduous incisor; I1 E/H/one – one or both first incisors erupting or half up and/or one only at full occlusal height; two-tooth – both permanent first incisors at full occlusal height and unworn, enamel wear or in wear; four-tooth, six-tooth and full mouth similarly for I2's, I3's and I4's; b.m. – broken mouth, i.e., one or more teeth shed (and see text)

*Fig. 8. Incisor eruption by age class.*

(Fig. 2). Outlying results, i.e. the extreme 2.5% at each end of the ranges, have not been excluded, but undue weight should not be given to them. Even excluding these, the range of stages observed, for example at 42 months, is very large, yet the central two-thirds of results are much less spread, from 6G to 7G/10G.

At twenty-four months, more than half of results were at 1/2A, that is, mandible stage E1/2. At 27 and 30 months, the summer and autumn of the third year, the median value is at 3/4A, with 1/2A still frequent. The posterior cusp of the third molar came into wear during the later part of the third year; by 3 years old, the median value was at 6G and few were still unworn at 3.5. The gradual change from stage 6G to 10G was seen from three to 4.5 years. The mature wear stage, 11G, was reached in two-thirds of cases at five years, and 84% by 5.5.

Replacement of the deciduous fourth premolar with the fourth premolar occurred later than M3 eruption. Compare the double underlined cells and the median values on Figs 6 and 7, and see Fig. 15 in the Appendix, 'Relative Wear', and the discussion of sheep and goats, below. For M3 at E/J, four-fifths retained dp4 and a fifth had dp4 shed or P4 erupting. By the time M3 reached 2A, premolar replacement was under way, with a fifth of P4s in wear. No individual was observed showing attrition on P4 while M3 was still not in wear (Figs 15 and 16 in the Appendix), but there were four cases of E/J in both P4 and M3, and two of P4 at E/H and M3 not yet erupted.

Note that the P4 results included 7.7% reversals (Fig. 2), mostly at the intermediate wear stages. Broadly speaking, 7S was reached during the third year, and the change from 7S to 12S occurred during the fourth and fifth year. The results are of limited usefulness for ageing.

Incisor eruption is shown on Fig. 8. Roughly speaking, four-toothed individuals were in their third year, six-toothed individuals in their fourth, and full-mouths were four years and older. From 27 to 48 months, there was a wide spread of eruption stages seen, but at 27 and 30 months more than half were four-toothed individuals, and at 36 months, more than half were six-toothed. From four years on, loss of incisor teeth – 'broken mouth' – was common, and in some cases it was uncertain whether the corner incisor (I4 or canine), was unerupted or shed, hence the category 'six/full b.m.' The process of eruption and coming into occlusion, 'I1 E/H/one', etc., was more spread in all four permanent incisors than for the cheek teeth.

Twenty-seven sheep without a known year of birth were observed at Butser. The most interesting of these were six Shetlands and one Soay that were already full mouths and with M3 at 11G when first seen. Four of these were seen over a two year period, during which time there was progressive erasure of the M1 infundibula, but only one case of erasure in M2, a Shetland ram reputed to be 9 or 10 years old. No cases of erasure were seen in M3 (mandible stage J) in any sheep.

### *The age of sheep observed at Payne's mandible stages*

The results as a whole are summarized on Fig. 9, grouped as described under Method, with subdivisions of Payne's mandible stages based on the results for the most recently erupted tooth. The columns were standardized, with the sample size shown below. At 12 months only four sheep were seen, and an estimated result was given, using the mean of the 11 and 13 months percentage results. Other irregularities have not been smoothed e.g. at 6 and 7 months, and 16 and 17 months). As before, the cell which includes the median value of each age class is bold and underlined. The cells which include the central two-thirds of results (33% either side of the median) are boxed, and

| Year | | | | | | | | | | | | | 1 | | | | | | | | | | 2 | | | | 3 | | 4 | | 5 | | 6 | | 7 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 24 | 27 | 30 | 33 | 36 | 42 | 48 | 54 | 60 | 66 | 72 | 78 | 84 | No. | |
| A | **100** | 34 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 24 | A |
| B | | **66** | **100** | **67** | 13 | (3) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 88 | B |
| C1/2 | | | | 33 | **76** | **68** | 5 | 10 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 80 | C1/2 |
| C3/4 | | | | | 11 | 28 | **69** | **79** | 22 | 10 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 98 | C3/4 |
| C5 | | | | | | (3) | 26 | 8 | **44** | 28 | 16 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 52 | C5 |
| C6+ | | | | | | | | (3) | 31 | **62** | **65** | **59** | 35 | 10 | | | | | | | | | | | | | | | | | | | | | | | | | 89 | C6+ |
| D1/2 | | | | | | | | | (3) | | 16 | 31 | **37** | **43** | 10 | | | | | | | | | | | | | | | | | | | | | | | | 51 | D1/2 |
| D3/4 | | | | | | | | | | | (3) | 10 | 27 | 43 | **69** | **76** | 46 | **53** | 13 | 8 | (9) | | (3) | | | | | | | | | | | | | | | | 115 | D3/4 |
| D5 | | | | | | | | | | | | | (3) | 5 | 15 | 18 | **38** | 34 | **52** | 31 | 36 | 7 | 9 | (2) | (2) | | | | | | | | | | | | | 69 | D5 |
| D6+ | | | | | | | | | | | | | | | 5 | (6) | 15 | 9 | 35 | **50** | **18** | **59** | 26 | 27 | 7 | (2) | | | | | | | | | | | | 77 | D6+ |
| E1/2 | | | | | | | | | | | | | | | | | | (3) | | 12 | 36 | 28 | **38** | **55** | 37 | 22 | 11 | 4 | | | | | | | | | | 85 | E1/2 |
| E3+ | | | | | | | | | | | | | | | | | | | | | | 7 | 24 | 14 | **51** | **50** | **50** | 34 | 7 | | 3 | | | | | | | 107 | E3+ |
| F5/8 | | | | | | | | | | | | | | | | | | | | | | | | (2) | (2) | 26 | 36 | **60** | **69** | 43 | 10 | (3) | (2) | | | | | 146 | F5/8 |
| F9/10 | | | | | | | | | | | | | | | | | | | | | | | | | | | | (2) | 10 | **31** | 13 | 14 | 6 | (5) | | | | 41 | F9/10 |
| F/G | | | | | | | | | | | | | | | | | | | | | | | | | | | (2) | | 10 | 14 | **27** | 25 | 8 | | | | | 47 | F/G |
| Ga | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 5 | 25 | **11** | **36** | 19 | 32 | (20) | | 57 | Ga |
| Gb | | | | | | | | | | | | | | | | | | | | | | | | | | | | | (1) | 7 | 21 | 47 | 48 | **71** | **64** | **60** | | 95 | Gb |
| H | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | (5) | (4) | (20) | | 3 | H |
| Totals | 12 | 35 | 25 | 51 | 38 | 40 | 58 | 39 | 36 | 39 | 37 | 39 | 4 | 61 | 39 | 17 | 39 | 32 | 23 | 26 | 11 | 29 | 34 | 44 | 41 | 46 | 44 | 50 | 86 | 42 | 67 | 36 | 50 | 21 | 28 | 5 | 1324 | |

Stages are defined on Tables 11 to 13. Ga – both M1 and M2 at 9A, M3 at 11G; Gb – M1 beyond 9A, M2 at 9A, M3 at 11G. Ageclasses are defined under Method. For each ageclass column, the median value is bold and underlined; the central two-thirds is boxed; the outlying 2.5% at each end and single outliers even if >2.5% are bracketed. Values for 12 months have been estimated, from the 11 and 13 months percentage results (actual data 2 at D1/2 and 2 at D3/4). Grouped stages have been allotted to adjacent stages, in the proportion of the adjacent stages (38 at C4/5, 20 at C5/7, 44 at D4/5, 7 at E3+/F and 5 at Ga/b). F/G is retained.

*Fig. 9. Percentage results for mandible stages by age class.*

| | A | B | C | D | E | E/F | F | F/G | G | H | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| decid nye | 6 | | | | | | | | | | 6 |
| **di1 present** | 18 | 88 | 320 | 129 | | | | | | | 555 |
| di1 shed, I1 nye | | | 2 | 5 | | | | | | | 7 |
| I1 E/H/one | | | | 30 | | | | | | | 30 |
| **two-tooth** | | | | 144 | 51 | | | | | | 195 |
| I2 E/H/one | | | | 5 | 34 | | 2 | | | | 41 |
| **four-tooth** | | | | 3 | 67 | 1 | 23 | | | | 94 |
| I3 E/H/one | | | | | 18 | 3 | 15 | 1 | | | 37 |
| **six tooth** | | | | | 15 | 1 | 65 | 9 | 3 | | 93 |
| six, b.m. | | | | | | 1 | | 3 | 3 | | 7 |
| I4 E/H/one | | | | | 2 | | 28 | 6 | 10 | | 46 |
| **full mouth** | | | | | | 1 | 40 | 23 | 74 | 3 | 141 |
| six/full b.m | | | | | | | 1 | 1 | 4 | | 6 |
| full, b.m. | | | | | | | 3 | 1 | 43 | | 47 |
| Total | 24 | 88 | 322 | 316 | 187 | 7 | 177 | 44 | 137 | 3 | 1305 |

*Fig. 10. Incisor eruption in relation to mandible stage.*

outliers (the 2.5% at each end of the range, and all outlying single records) are in parentheses. Reading across the table, there is a normal pattern of increasing and decreasing values, with the columnar median in the central parts of the rows. The subdivision of F is interesting, with the central two-thirds of F5/8 at 2.5 to 4 years (146 results), and of F9/10 at 3.5 to 4.5 (41 results), a useful distinction, at the prime of a sheep's life.

The main Payne stages are shown in relation to incisor eruption on Fig. 10.

### *Breed comparisons*

A summary of results by breed and breed group is shown in Figs 11–13 in the Appendix using the subdivided mandible stages. Grouped results, for example C5/7, were allotted to adjacent stages proportionally to the nearest whole number. Each main symbol represents two records. The Scottish Blackfaces are shown on separate columns on Figs 11 and 12, as they span more than one age class. The older ones are included with the rest. They are more tightly aged, e.g. the 54 months age class covers six months (51 months, 1 day – 57 months, 0 days), and the Blackfaces are aged two or three weeks either side of 52.5 months. The Blackfaces have good sample sizes up to 6.5 years. Some older commercial sheep were seen, as CFP did not have many older sheep of traditional breeds (see also Fig. 1). Note, when reading the tables, the greater reliability of data in the columns than in the rows (see Method). To save space, the Shetlands, White-faced Woodlands, Hebrideans, Manx Loghtans, Jacobs and others, from both CFP and Butser, were combined to an 'Other minority' group. There is variation within these, but they are all traditional or rare breeds which have not been bred with improved breeds in the recent past (at least the last 60 years, E. Henson, pers. comm.). (For simplicity they are referred to as a breed not a breed group, below).

The important question is whether there are large differences in the results from different breeds and farms. There has long been an uncertainty about whether animal breeding in the last two hundred years has caused an acceleration in eruption timing, as some studies have suggested (see Deniz and Payne 1979, Table 6), although other work suggests this has been exaggerated. Bull and Payne (1982, 65) discuss Brown's 1902 edition of his book on the dentition of farm animals in which Brown comments that no change in the rate of development of the teeth of cattle, sheep or swine had been seen in the 50 years since the 1860 first edition (and see Payne 1984, and Legge and Dorrington 1985, 130–131).

Fig. 11 shows the first year results. Overall, the general similarity of the pattern for all sheep is noted. At eight of the 12 age classes, the mode (highest value) for each breed was at the same mandible stage. The Scottish Blackfaces confirm the similarity, from a different breed and geographical area. At 4.5 months, most are at C1/2, as are the other breeds at 4 and 5 months, with a few at C3/4, as would be expected from the 5 months results. At 10–11 months, results were intermediate between the minorities at 10 months and 13 months. At 16–17 months and 22–23 months (Fig. 12), and at later ages (Fig. 13), they show a pattern similar to the minorities. At all these points, the Blackfaces show a narrower spread of stages than the records as a whole.

The Soays and Mouflons, as the most primitive of the breeds seen, may be expected to be rather different (Clutton-Brock *et al.* 1990). Yet for nearly all age classes, the mode for the Soays is at the same stage as the results overall. There is, however, a regular tendency for some Soays to be at earlier stages, and none at later stages of each age class. As each molar tooth erupts, most Soays are the same as the minorities, but there are a few not reaching the early-wear stage, at the age where all other breeds have reached C1/2, D1/2 or E1/2 respectively, see, for example, the Soays still at B at 4 and 5 months (five individuals), or still at D5 or D6+ at 24 to 30 months. Note the similarity in the results, though, at 9 and 10 months, and 3.5 to 6.5 years.

Three Mouflons were examined, two ewes (9 and 12 records) and a ram (3 records), and a Mouflon cross Soay (6 records; aged 3 to 15 months, i.e. the records later than 15 months are all Mouflon). The Mouflon records were mostly at the mode for Soays, sometimes at one stage earlier, but almost always within the range of Soays examined. An example is the Mouflon and a Mouflon x Soay with M2 not yet in wear at 13 months. (The Mouflon record at D3/4 at 22 months is probably an error, as this sheep was at E1/2 at 24 and 27 months).

At 6 and 7 months, there is a difference within the Soay results with four records at C5 at 6 months, and only one at 7 months, which was a result of missing a six months visit one year and a seven months visit the next: an example of variation due to season or management within one farm and breed.

A few commercial sheep were seen. The few younger

sheep examined included eight at 3 months, none of which showed wear on M1, though all had M1 erupting (anterior element erupting or half-up and posterior element unerupted). Other records were also within the range seen overall but tending towards the later stages at each age class, excepting for the three cases at stage H, M2 beyond 9A.

The first case of wear on M3 was in three minorities, a Butser Manx Loghtan ram, a CFP Shetland ram, and a CFP White-faced Woodland ewe, at 19 months, and four commercial ewes at 20 months, with an increasing proportion of minorities with M3 in wear at 21 and 22 months. No Soays showed wear on M3 until 24 months, when 8 of 14 (57%) were in wear compared to 77% of 31 Blackfaces at 22/23 months. At 27 and 30 months, five Soay records (three individuals) were the only sheep with M3 still not in wear.

Looking at the older sheep (27 months to 7 years), in eight of the 12 age classes the mode for the minorities, Blackfaces and Soays were at the same mandible stage. The Soays, again, have a higher proportion at earlier stages, but most are at F/G or G by 4.5, as are the Blackfaces. By 5.5 almost all Soays had reached G. The older commercial sheep examined at 5.5 to 6.5 were almost all at G, with one case each at 6 and 6.5, plus the single record at 7 years, at stage H. The four minority breed records (four individuals) at 7 years were still at stage G (one at Ga and three at Gb).

### *Sex differences*

No difference was seen between ewe and ram lambs in the age at which C1/2 and C3/4 was seen. Only at Butser were any older rams seen. Of 51 individuals at stage D and beyond, 14 were rams, and 37 ewes. The earliest record of D1/2 was in two ewes, at 11 months (a Hebridean and a Shetland). The earliest five records of D3/4 were a Soay ewe at 10 months and four rams at 11 and 12 months (four different individuals, a Shetland, Hebridean, Soay and Manx Loghtan). One of these four rams, the Manx Loghtan, was the earliest record of E1/2, at 19 months. The range of stages seen at 13 and 24 months is shown on Fig. 14. Numbers are not large enough to be very useful.

### *Relative wear*

The wear on earlier erupting teeth in relation to later erupting teeth has been used in ageing studies (e.g. Grant 1978, Grant 1982 especially Table 3, Deniz and Payne 1982, 193–196, and, for humans, Miles 1963, 2001) and may be used to study wear-rate, and to study sheep/goat differences (see below). The wear of one tooth in relation to earlier erupting teeth are shown on Fig. 15. Taking the row or column of one stage of the later erupting tooth, the stages seen in the earlier tooth can be read. The median is bold and highlighted. In archaeological samples the rate of wear can be recorded as slower, similar, faster, or much faster than that seen here. For example, each mandible may be recorded as less than, equal, beyond or well beyond the median value, or even outside the range (see discussion of the Makrigialos sample, below). If the wear-rate appears fast in younger mandibles, this will be useful in judging whether very worn older jaws are the result of wear or age (but see also Sheep/goats). High wear rate is likely to be the result of high soil ingestion (Nolan and Black 1970, Healy and Ludwig 1965), and this may allow inferences to be made about stocking rate, pasture shortage, or pasturing on arable land, for example, sheep-folding on fallow.

The wear-rate figure may be useful in estimating stage in incomplete archaeological mandibles.

### *Sheep/goat differences*

The striking difference observed between sheep and goats is in the wear rate of dp4 and the timing of eruption of P4. The deciduous premolar is lower crowned in goats (see Fig. 3, Payne 1985) and therefore erasure of the infundibula and replacement by the permanent tooth occurs sooner. Both Habermehl (1975) and Silver (1969) gave earlier P4 replacement times for goats than sheep. In Deniz and Payne's study of goats, stage 16L was reached in half of the records at six months (Deniz and Payne 1982, Fig. 20), whereas in the sheep studied here, this did not occur until 15 to 20 months. 14L was a much more frequent record than 16L in sheep (305 records of 14L and15K, and 97 of 16L), which was the reverse in goats (58 at 14L, 182 at 16L), i.e., in goats the anterior infundibulum was beginning to erase soon after all dentine joins were complete. Eruption of M3 and P4 in the sheep is described above and relative stages are shown on Fig. 15. In goats, the approximate average eruption of M3 was 25 months and for sheep it was 21 months, while for P4 eruption the figures are a nearly exact reversal (Fig. 16), that is, in goats it is the permanent premolars which erupt during the second winter, whereas in sheep, it is the third molar. It may well be important for goats to have functioning premolars when the spring browse appears. Relative eruption of M3 and P4 at stages E/J and 1/2A, and probably also at 3/4A, look to be useful indicators for separating sheep and goats, in addition to the work done on young lambs and kids (Payne 1985) and permanent premolars and molars (Halstead *et al.* 2002).

Differences in the ease of use of the speculum was referred to in the 'Accuracy' section above. Goats, being browsers, open their mouths wider. As an aside to this point, the morphology of the mandibular condyle in sheep and goats may reflect this difference. The posterior facet at the lingual corner of the condyle is usually larger in goats.

Of the morphological differences between lambs and kids observed by Payne, the shape of the metaconid of

dp3 and the ridge arising from it was the character most easily seen in live sheep (Payne 1985, Fig. 2: 3b). Observations of twenty 4.5 months old Blackfaces confirms the description given for lambs, with the ridge connecting to the posterior part of the tooth.

## Discussion

In drawing conclusions from the results, the difficulties and inaccuracies described should be kept in mind. However, the correlation of mandible stage with age class in Fig. 9 is strong. For single breeds, the Scottish Blackfaces alone or the Soays alone, the range of stages seen at each age was narrower than overall, and this is also likely to be true of archaeological samples.

Using Payne's A, B, C…J stages, in general terms, stage A records were lambs a few days or weeks old, stage B were one to three months, stage C three/four to 12 months, stage D were yearlings and stage E was reached at the end of the second year. Excluding single outliers, during the first two years there are eleven months in which all sheep examined were of a single stage: stage B at two months, stage C at five to nine months and stage D at 14 to 18 months.

Eruption of the first molar at three months is confirmed, with wear beginning at 3 and 4 months. This figure is quoted by most authors, and was similar for goats (Deniz and Payne 1979, 1982). Second molar eruption is given as 9–12 months by some authors (Silver 1969 and Sisson & Grossman 1953, quoted in Deniz and Payne 1979, Table 6), which matches well the results presented here with initial wear at 10–13 months, and was similar for goats. Several authors give 9 months (e.g. Habermehl 1975, Miller and Robertson 1959). This is correct for 'first signs of eruption': at 9 months less than half were erupted, and at 10 months more than half were erupted. Third molar eruption was widely spread at 18 to 27 months, which is similar to 18 to 24 months given by Silver and Sisson & Grossman. Other authors give 18 months, and as with M2, this would be true for the first signs of eruption in some sheep. The 1790 'semi-wild hill sheep' figure of Silver's is not close to results here for any of the three molar teeth (unless eruption was taken to mean 'in occlusion on all cusps', 4A for M1 and M2 or 6G on M3, in which case they are close for M1, late for M2 and comparable for M3). There is confirmation, therefore, of the quality of 19th century research, and of Brown's 1913 observation.

The mandible stages could be labeled as shown in Fig. 17 for use in histograms and survivorship curves (e.g. Dobney *et al.* 1996, Fig. 52a–e). Subdivision of the histogram bar, as described above ('Mandible stages'), would preserve the general pattern, which would be obscured by using a bar for each subdivision if sample sizes are not large; it would also show some primary data. The survivorship curve could use the subdivided stages without loss of clarity. If points are labeled with the 'central point', it should be made clear that the stages overlap, and the 'majority' or 'all records (except outliers)' figures quoted. The points are neither a linear nor a logarithmic scale, but they do show detail at the points of greatest interest. It would aid clarity if, for example, the 3, 6, 12, 24 months, 3 and 4 year points could be shown on the outer part of the frame of the figure.

The probable age of archaeological mandibles could be calculated from the figures in Fig. 9 (Chamberlain, pers. comm., Buck *et al.* 1996, Chamberlain 2000). Taking the row at mandible stage C3/4 as an example, the percentage values, at 4 to 9 months, summed and normalized, give probabilities of 0.050, 0.128, 0.315, 0.361, 0.100 and 0.046 for the six age classes. If the assumption is made that all ages are equally likely (the 'uniform prior'), the ten mandibles at stage C3/4 might be allotted to the six ages classes thus: 0.5, 1.28, 3.15, 3.61, 1 and 0.46, or, to the nearest whole sheep: 1, 1, 3, 4, 1 and 0. If this method is applied to whole mandible samples, some smoothing of irregularities in the data may be advised, and the correct probability value needs to be applied at the three-months and six-months age classes; (e.g. to keep the 'uniform prior', the series at stage E3+ is: 7, 24, (14x3), …(34x6)…). Estimated values would be needed for mandibles showing stage A, which may include pre-natal deaths, and the later stages, G, H and J. In estimating values for the late stages, assumptions have to be made about likely survivorship, and a 'model prior' may be necessary (an old sheep is more likely to be nine than 13 years).

A meaningful, yet space-efficient, way of showing primary tooth wear stages in archive tables, is to make a table comparable with Grant's Table 3 (Grant 1982), but with the major stages as the columns, A+B, C, D, etc., and the tooth stage combinations, ordered, in each column. Payne's stages are sometimes abbreviated by removing the suffix, '2' instead of '2A', which for most teeth means only a small loss of information; but for M3 the suffix is needed, to show whether the posterior cusp is in wear.

### *Seasonality*

The spread of ages for each stage during the first year is small enough to be useful in studies of season of death in archaeological samples, with some helpful information for the second year.

Lambing time for sheep seen is given above ('Tagging and date of birth'). Lambing is later within the UK as latitude and altitude increases. Hafez (1969) quotes later February and March for southern British sheep, but this is earlier than in the sheep examined here, and the St. Kilda Soays. Lambing normally occurs over about a five week period. If a presumption is made that lambing occurs from 1st to 30th April, during July lambs would be aged

2 months, 0 days to 4 months, 0 days, i.e. half would be age class 3 months, and a quarter would be in each of age classes 2 and 4. Or put the other way, the 3 month age class (2 months, 16 days to 3 months, 15 days) would occur from mid June to mid August. The six months class would occur from mid September to mid November, and the nine months class from mid-December to mid-February. Deaths during February would show the stages seen at ten months (50%) and nine and eleven months (25% each).

Taking this presumed lambing time and the central two-thirds of results on Fig. 9, mandibles at C1/2, three to five months of age, are in the summer of their first year, and those at C3/4, five to eight months, are in the autumn or early winter. C5, six to nine months, are autumn or winter, and C6+, eight to twelve months, late autumn to spring (defining summer as June to August, autumn as September to November, winter as December to February and spring as March to May). Early wear on M2, D1/2, at 10 to 13 months, would be seen in winter and spring, and could be winter losses or yearling spring lamb. Estimates can be suggested for stages D3/4 to E1/2, but with a wider range. A more detailed presentation of the ranges could be given by using probabilities, as referred to above. Where there are young lambs, use of Figs 1 and 2 will allow finer ageing, from early wear stages of dp4, and eruption of M1. Mandible stage B could be divided into 'Ba', 'dp4 in wear, M1 unerupted', two months or less, and Bej, 'dp4 in wear, M1 erupting', probably 3 months old (Fig. 2)(erupting, for live sheep, is a little more advanced than Ewbank *et al.*'s E).

### *Comparative sources*

Payne's 1973 estimates for the mandible stages are shown on Fig. 17 as they have been widely quoted, even long after the goat study was published. In broad terms, the estimates were good. The main adjustments indicated are the earlier beginning to stage C, the considerable overlap of stages, and the higher upper limits of stages E, F and G. The Turkish Angora goats, shown in the final column of Fig. 17, were very similar to the study sheep up to the beginning of stage G. The goats were about a month later at the C to D transition, and as shown above, somewhat later at the D to E transition. Goats reached the latest mandible stages earlier than the sheep.

In the sheep, few cases of late wear were seen in M2 and none in M3, stages H and J, primarily because so few old sheep were seen. There is some information about older sheep from other studies, see Fig. 18. In the St. Kilda Soays (Clutton-Brock *et al.* 1990) and the Shetland sheep studied by Davis (1996 and 2000), the first cases of Stage H were, as in the present study, at six years of age. Some earlier cases were found in Moran and O'Connor's study of sheep in museum collections (1994, and pers. comm.). Cases of Stage J, where M3 is wearing to the base, were not seen in the St. Kilda Soays nor in the study sheep. One of the Shetland six-year olds was at Stage J, as were several eight and nine-year olds in the museum study.

Further study of older sheep is needed, both in tooth wear stages seen in known-age older sheep, and in estimating the upper limit used for stages H and J on Fig. 17. The age of the live population of registered Rare Breed sheep in January 2003 is shown on Fig. 20, (E. Henson, Grassroots System, pers. comm.), a very large and interesting data-set from the Rare Breeds Survival Trust. For these sheep, the normal life-span is up to nine or ten years, though numbers reduce somewhat at six to eight years. The nine and ten year olds will be described by the farmers as 'old'. Sheep of 11 to 13 are few, and over 13 rare, with the oldest nearly 19 – all may be described as very old. Some aspects of the age structure of these sheep may be typical of sheep generally, e.g. that few live beyond ten. Other aspects are probably not typical, for example in the keeping of ewes so long, which maximizes the progeny from each sheep, and contributes to the survival of the breed. The very old sheep will certainly include some that have become pets. On modern hill farms in the UK, sheep over 7 years old are unusual, but lowland farms often keep their best ewes a year or more longer, if still with good teeth and udders and still producing twins and triplets (Griffith, pers. comm.).

Of the mandibles from St. Kilda (Clutton-Brock *et al.* 1990), all the records were within the range seen in the present study, except for one M3 at 10H at 11 years.

The mandible stages of the Shetland sheep studied by Davis (1996, 2000) were compared with the study results (Fig. 9). They were within the range of stages seen, except for one at 15 months with M2 only just in wear. For those up to three years old (all rams and castrates), most were at the stage which includes the median value, with some cases one stage earlier or later and only one two stages later (seven one stage earlier, 20 equal to, six one stage later, and the one two stages later). Those over three years (8 wethers and 26 ewes) tended to be one stage later (two one stage earlier, six equal to, 17 one stage later, and one two stages later). More of the Shetlands had reached Gb, where M1 is beyond 9A, at 4.5 years (55 months) than in the study sheep, and more had reached stage H at nearly 7 years (79 months).

In Moran and O'Connor's study, all the results for dp4 and P4 quoted are within the ranges seen. For M1, all are within the range except the 44 months old Gotland castrate at 15A. For M2, most records are within the range, but 8A/B was not normally reached by 18 months, and the M2 at 15A at 72 months is earlier than seen in this study. The description of results for M3 show a few cases outside the range seen here, viz. the 36 months old Soay with M3 erupting and not yet in wear; C51 with M3 at 11G at 32 months and the Soay castrate (82:574) at 11G at 36 months: both very early; and, as suggested, WM30 was probably wrongly aged.

Payne's sample of modern Turkish sheep, all

slaughtered in February 1972 (1973, Fig. 14), included five estimated to be 9–12 months and three 21–24 months. These all look correctly estimated. Of the older sheep, one, 'KAR 1', could be rising 2 or rising 3. The others were all at stages G, H or J, half of them beyond G, which is in contrast to the results here, see Fig. 19.

### *Grant's tooth and mandible wear stages*

Grant's tooth wear stages (1975, 1982) are similar to Payne's. The work here suggests that it is worth adding a stage between 'b' (equivalent to '2A') and 'c' (equivalent to 5A) so that stage 4A is recorded separately, i.e. four cusps in wear (six for dp4) with dentine not continuous anteriorly. Grant's stage 'h' needs to be used with caution, making it clear whether the stage seen implies that the infundibulum is nearly worn to the base, or whether the infundibulum is just of an unusual shape. In Fig. 19, this latter interpretation is made, and 'h' is included within Payne stage 9A. Because in live sheep one cannot see the earliest stages before the tooth is visible in the mouth, the mandible wear stage (MWS) could not be calculated until all three molar teeth were visible. The MWS could be calculated for 567 records, although this required giving a single figure for grouped values (e.g. 11.5 for 8A/9A). Median values were MWS 29 at 24 months, 31 at 30 months, 33 at 3 years, 34 at 4 years, 38 at 5 years and 39 at 6 years. Because the eruption and early wear stages are less variable than late wear stages (see Figs 3 to 6) and tooth wear stage 'g' is so long-lasting, it was considered more sound to base stages on the most recently-erupted tooth where possible. The detailed presentation of results (Grant 1982, Table 3) is very valuable, and it is recommended that individual mandible results should be published.

### *Some archaeological examples*

A detailed study of archaeological samples is beyond the scope of this study, but an example of the use of the results is taken by looking at older sheep. Age estimates for late stages need to use information about relative wear rates, and assumptions about likely survivorship. Payne's modern Turkish sheep sample and the archaeological sample from Asvan Kale both included about equal numbers at stage G and stage 'H plus J', see Fig. 19. The same is so for the much larger sample of sheep from late Neolithic Makrigialos, Greece (Halstead, pers. comm.). At the UK archaeological sites (summarized by Grant 1982, Table 3), however, a much lower proportion were at H or J, and the same was so for medieval sheep from Lincoln (Dobney *et al.*1996) (Fig. 19). Are the Turkish and Greek sheep older, or are their teeth wearing down faster, and reaching H and J sooner?

The use of the Relative Wear table (Fig. 15) is useful in considering this question. For the sheep from Makrigialos, a cross-tabulation of dp4 and M1 shows that at every wear stage of M1 (not shown, sample size 132), the mode stage for dp4 is at a later wear stage than the mode for the study sheep. Taking eruption as being less variable than wear, it can be suggested that wear-rate is faster for the Greek sheep. Somewhat earlier age estimates may therefore be suggested for the mandible stages which depend on wear. Consideration could be given to using C5+ and Cej as the final two subdivisions of C (see 'Mandible stages', above). The comparable dp4 by M1 cross-tabulation for goats confirms the faster wear of goat deciduous teeth, with all cases beyond the mode, and more than half (9 of 16) beyond the range seen in the study sheep. A further line of enquiry is to compare the number of cases of M1 worn beyond 9A before M3 has reached 11G. In the Makrigialos sheep, M1 was usually already beyond 9A before M3 reached the mature-wear stage, and consequently there were few records in the stage Ga (Fig. 19). This is in great contrast to the study sheep, and usefully indicates faster wear rather than older sheep in the Greek sheep sample reflecting the drier climate in Greece, and the greater soil ingestion (for references see 'Relative wear' above).

Returning briefly to Grant's UK material, this last comparison shows an intermediate position, with M1 relatively more worn than the study sheep, but less worn than the Greek sheep.

### *Aspects for further study*

A number of aspects of the sheep data have not been presented, for example the wear stages of incisor teeth, the detailed tooth stages for dp4, dental anomalies, the differences between breeds for incisors, and differences within the minority breeds and between the Scottish Blackface farms. The study lacked good data for rams and castrates, and older sheep. A more detailed comparison of the sheep and the Turkish Angora goats would be of interest. There may be variation in tooth size and shape, for example, in the depth of the folds on which the intermediate wear stages are based, and the depth of the infundibula.

## Conclusions

In conclusion, the study suggests that age estimates for tooth eruption in archaeological material may be made with considerably more confidence than has been the case previously. The 19th century data, on which we have relied rather tentatively in the past, have proved reliable. The amount of variation is quantified, and methods of analysis need to bear this variation in mind. The subdivided mandible stages used for the overall summaries in Figs 9 and 17 are valuable. Of these stages, those which depend on early wear of the latest-erupted tooth provide information almost as reliable as for eruption, and these include many of the stages up to three years old. Tooth

eruption in goats is very similar, but with the difference in the order of eruption of P4 and M3.

Mandible stages which depend on later-wear of individual teeth are in a different category, as the age of reaching these stages depends on how fast the teeth wear. Study of relative-wear suggests that the teeth of the study sheep, kept mostly on permanent pasture, wear more slowly than UK Romano-British to medieval sheep, and considerably more slowly than Neolithic Greek sheep. Age estimates may therefore be adjusted, on an informed basis.

*Acknowledgements*

Grateful acknowledgement is made to Sebastian Payne for practical help and later discussion; to Joe Henson at the Cotswold Farm Park, the late Peter Reynolds at Butser Ancient Farm and John Spence at the Animal Diseases Research Association, The Moredun Institute; and their staff, especially Robert Boodle and Alex Wyman; to numerous sheep helpers, in particular, Andrew King, Martin Morris, Sheila Raven and John Giorgi; to the British Academy and the Robert Kiln Trust for funding part of the practical work; to Bob Wilson, Bruce Levitan, Andrew Speedy, Barry Cunliffe, Sunny Dawson, Keith Dobney, Paul Halstead, Andrew Chamberlain, Simon Dobson, Terry O'Connor, Simon Davis, Peta Sadler, Judy Griffith, Elizabeth Henson and Andrew Millard for discussion and help on various aspects of the work; to Derilyn Frusher for typing records into the database while a student at Sheffield University, to the Rare Breeds Survival Trust for the information about the age of live sheep, and to Paul Halstead for information from Makrigialos.

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# Appendix

| Stage | | Ageclass/ Breed | 0 | 1 | 2 | 3 | 4 | 4½ Sc. Bl. | 5 | 6 | 7 | 8 | 9 | 10 | 10¾ Sc. Bl. | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **A** | dp4 not yet in wear | Soay<br>Other min.<br>Sc. Blackf. | ●<br>■•<br>♦♦♦ | ●●●●<br>■ | | | | | | | | | | | | |
| **B** | dp4 in wear, M1 not yet in wear | Soay<br><br>Moufl, MxS<br>Other min.<br><br>CFP cross | | ●●●●●<br>●<br><br>■■■■■• | ●●●●●<br>●●●<br>•<br>■■• | ●●●●●<br>●<br>•<br>■■■■■<br>■<br>✞✞✞ | ●●• | | • | | | | | | | | |
| **C1/2** | M1 anterior cusp(s) only in wear | Soay.<br><br>Moufl, MxS<br>Other min. | | | | ●●<br><br>■■■■■<br>■• | ●●●●●<br>●•<br><br>■■■■ | <br><br>♦♦♦♦♦<br>♦♦♦• | ●●●●●<br>●●•<br>•<br>• | ●• | ●● | | | | | |
| **C3/4** | M1 at 3/4A, M2 not yet in wear | Soay<br><br>Moufl, MxS<br>Other min.<br><br>CFP cross | | | | | • | <br><br>♦• | ●•<br>•<br>■■■ | ●●●●●•<br><br>■■■■■<br>■■■■■<br>■■<br>✞✞• | ●●●●●<br>●●<br>•<br>■■■■■<br>■•<br>✞ | ●●•<br><br>•<br><br>✞ | | | | |
| **C5** | M1 at 5A, M2 not yet in wear | Soay<br>Moufl, MxS<br>Other min.<br>CFP cross | | | | | | | • | ●●<br><br>■■■■•<br>• | •<br><br>■ | ●•<br>•<br>■■■■■•<br>✞ | ●•<br><br>■■■<br>✞ | •<br><br>■■■ | | |
| **C6+** | M1 at 6A or more, M2 not yet in wear | Soay<br>Moufl, MxS<br>Other min.<br><br>CFP cross | | | | | | | | | • | ●•<br><br>■■<br><br>✞✞ | ●●●●●•<br>•<br>■■■■•<br><br>✞• | ●●●●●<br>○<br>■■■• | ♦♦♦♦♦<br>♦ | ●●●●●•<br>•<br>• |
| **D1/2** | M2 anterior cusp(s) only in wear | Soay<br>Other min.<br>CFP cross | | | | | | | | | | • | | ■■• | ♦♦♦♦♦• | ■ |
| **D3/4** | M2 at 3 or 4A M3 not in wr | Soay<br>Other min. | | | | | | | | | | | | • | • | ■• |

Each main symbol represent two records. ● Butser Soays, ○ Mouflon or Mouflon cross Soay, ■ Other minority breeds, ◆ Scottish Blackfaces and ✞ Cotswold Farm Park (CFP) commercial crossbreds; • represents one record, e.g., ●●●• represents seven Soay records. Soay cross Suffolks are not shown. Records at grouped stages, C4/5, C5/7, D4/5, E3+/F and F7/10, were allocated in the proportion of the adjacent stages, to the nearest whole number. Scottish Blackfaces are given their own column for the first and second years.

*Fig. 11. Mandible stages by breed, age classes 0 to 11 months, each main symbol representing two records.*

| Stage | | Ageclass/ Breed | 12 | 13 | 14 | 15 | 16 | 16½ Sc. Bl. | 17 | 18 | 19 | 20 | 21 | 22 | 22¾ Sc. Bl. | 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **C6+** | M1 at 6A plus M2 unworn | Soay<br>Moufl, MxS | | ●●<br>○ | | | | | | | | | | | | |
| **D1/2** | M2 anterior cusp(s) only in wear | Soay<br>Other min.<br><br>CFP cross | •<br>• | ●●●<br>■■■■■<br>■■■■•<br>• | ●<br>•<br><br>• | | | | | | | | | | | |
| **D3/4** | M2 at 3/4A<br>M3 not yet in wear | Soay<br>Moufl, MxS<br>Other min.<br><br><br>CFP cross | •<br><br>• | ●<br>•<br>■■■■■<br>■■■■■<br>■ | ●●●<br><br>■■■■■<br>■■■■•<br><br>✞ | ●●•<br>•<br>■•<br><br><br>✞• | ●<br><br>■■■■ | ♦♦♦♦♦<br>♦♦♦ | ●●<br>•<br>■<br><br>• | ●• | •<br><br>• | • | | • | | |
| **D5** | M2 at 5A,<br>M3 not yet in wear | Soay<br>Moufl, MxS<br>Other min.<br>CFP cross | | <br><br>■• | <br>■<br>✞✞ | <br><br><br>✞✞ | ●<br><br>■■■<br>✞✞✞ | <br><br>♦♦ | ●●•<br><br>■•<br>✞• | ●●•<br><br>■■•<br>✞ | ●●•<br><br>■■ | ●● | •<br><br>• | ●•<br>• | | ● |
| **D6+** | M2 at 6A or more,<br>M3 not yet in wear | Soay<br>Moufl, MxS<br>Other min.<br>CFP cross | | | <br>•<br>• | <br>• | <br><br>■■<br>✞ | | •<br><br>• | ●•<br><br>■•<br>✞ | ●<br><br>■■■■■ | •<br><br><br>• | ●●●<br><br>■■■■■• | ●●<br><br>■ | <br><br>♦♦♦• | ●•<br>•<br>• |
| **E1/2** | M3 anterior cusp(s) only in wear | Soay<br>Moufl, MxS<br>Other min.<br><br>CFP cross | | | | | | | | | ■• | <br><br><br>✞✞ | ■■■■ | ■■■■■• | ♦♦♦♦♦<br>♦♦♦♦ | ●●●<br>•<br>• |
| **E3+** | M3 central cusp(s) in wr, distal unworn | Soay<br>Other min.<br>CFP cross | | | | | | | | | | | ■ | ■■■• | ♦♦• | ● |
| **F5/8** | M3 5G to 8G | | | | | | | | | | | | | | • | |

Each main symbol represents two records.

*Fig. 12. Mandible stages by breed, age classes 12 to 24 months.*

| Stage | | Ageclass/ Breed | 27 mo | 30 | 33 | 3 yr 36 | 42 | 4 yr 48 | 54 | 5 yr 60 | 66 | 6 yr 72 | 78 | 7 yr 84 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **D5** | | Soay | • | | | | | | | | | | | |
| **D6+** | | Soay | ●• | • | | | | | | | | | | |
| **E1/2** | M3 anterior cusp(s) only in wear | Soay<br>Moufl, MxS<br>Other min.<br>Sc. Blackf<br>CFP cross | ●●●•<br>•<br>■■<br>♦<br>• | ●●<br><br>■•<br>♦•<br> | ●●<br><br>•<br><br> | •<br><br><br>•<br> | | | | | | | | |
| **E3+** | M3 central cusp(s) in wear, distal cusp unworn | Soay<br>Other min.<br><br>Sc. Blackf<br>CFP cross | ●●<br>■■■■•<br><br>♦♦♦<br>✞ | ●●●•<br>■■■■■•<br><br>♦♦•<br> | ●●●●●<br>■■■■■<br>■<br><br> | ●●●•<br>■■<br><br>♦♦•<br> | ●•<br>•<br><br>♦<br> | | ■ | | | | | |
| **F5/8** | M3 distal cusp in wear, 5G to 8G | Soay<br><br>Moufl, MxS<br>Other min.<br><br>Sc. Blackf<br><br>CFP cross | <br><br><br>•<br><br><br> | ●<br><br><br>■■■■•<br><br><br>• | ●<br><br><br>■■■■■<br>■■<br><br> | ●●•<br><br><br>■■■■<br><br>♦♦♦♦♦<br>♦♦♦♦ | ●●●●●<br>●●●•<br><br>■■■■■<br>■■■■■<br>♦♦♦♦♦<br>♦•<br>✞✞✞✞ | ●●<br><br><br>■■<br><br>♦♦♦♦♦<br> | <br><br>•<br><br><br>♦♦• | <br><br><br>•<br><br><br> | <br><br><br>•<br><br><br> | | | |
| **F9/10** | M3 distal cusp in wear, 9G to 10G | Soay<br>Moufl, MxS<br>Other min.<br>Sc. Blackf<br>CFP cross | | | | <br><br>•<br><br> | <br><br>■■<br>♦<br>✞✞ | <br>•<br>■■<br>♦♦♦♦<br> | ●<br>○<br>■<br>♦•<br>• | <br><br><br>♦♦•<br> | ●<br><br>•<br><br> | <br><br><br>•<br> | | |
| **F/G** | | Soay<br>Moufl, MxS<br>Other min.<br>Sc. Blackf<br>CFP cross | | | <br><br>•<br><br> | | •<br><br>■•<br>♦•<br>✞ | •<br><br>■•<br>♦<br> | ●●•<br>•<br>■<br>♦♦♦♦<br>• | ●•<br>•<br>•<br>♦♦<br> | <br><br>•<br>♦•<br> | | | |
| **G** | M3 at 11G, M2 at 9A | Soay<br>Moufl, MxS<br>Other min.<br>Sc. Blackf<br><br>CFP cross | | | | | •<br><br>•<br>•<br><br>• | •<br><br>•<br>♦•<br> | ●●●<br><br>■■■■•<br>♦♦♦♦♦<br>♦♦<br>• | ●•<br><br>■•<br>♦♦♦♦♦<br>♦•<br>• | ●●●●<br>•<br>■<br>♦♦♦♦♦<br>♦♦♦♦♦•<br>✞✞✞✞• | ●●<br>•<br>■•<br>♦♦♦•<br><br>✞✞ | ●•<br><br><br>♦♦♦♦♦•<br><br>✞✞✞✞✞<br>✞• | ■■ |
| **H** | M3 at 11G, M2 > 9A | CFP cross | | | | | | | | | | • | • | • |

Each main symbol represents two records.

*Fig. 13. Mandible stages by breed, age classes 27 to 84 months.*

| | 13 mo | | | 24 mo | |
|---|---|---|---|---|---|
| | f | m | | f | m |
| C6+ | 4 | 2 | D5 | 1 | |
| D12 | 20 | 5 | D5/7 | 3 | |
| D34 | 20 | 3 | D6+ | 7 | 2 |
| D4/5 | 3 | | E12 | 20 | 4 |
| D5 | 1 | 1 | E3+ | 5 | 1 |
| D5/7 | 1 | | F5/8 | 1 | |

Butser sheep, mixed breeds.

*Fig. 14. Mandible stages observed in ewes and rams of 13 and 24 months.*

| | | | | | | | | | | | **P4** | **dp4** | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 8 | | | | | | | | | | shed | shed | | | | | | 1 | 4 | | | | | | | | |
| | 3 | | | | | | | | | | 15A | 21/23 | | | | | | 1 | 16 | | | | | | | | |
| | 29 | | | | | | | | | | 14S | 20 | | | | | | 9 | 13 | | | | | | | | |
| | 114 | 17 | 13 | 11 | 5 | | 1 | 1 | | | 12S | 18/19 | | | | | | 10 | 16 | | | | | | | | |
| | 5 | 2 | 1 | 5 | 3 | | 1 | 1 | | | 9A | 17 | | | | | 4 | 17 | 20 | | | | | | | | |
| | 6 | 5 | 4 | 10 | 1 | | 1 | | | | 5/12W | 16L | | | | | 9 | 44 | **39** | | | | | | | | |
| | 4 | 6 | 8 | 23 | 12 | 0 | 5 | 2 | | | 8A | 15K | | | | | 14 | **25** | 13 | | | | | | | | |
| | 1 | 4 | 4 | 30 | 12 | 1 | 7 | 15 | 2 | | 7S | 14L | | | 2 | 32 | **42** | **57** | 76 | 39 | | | | | | | |
| | | | | 3 | 1 | | | | | | 4A/7S | 10/14 | | | 5 | **33** | 9 | 4 | | | | | | | | | |
| | | | | 2 | 1 | | 3 | 2 | 1 | | 4A | 13L | | 2 | 8 | 10 | 7 | 1 | | 1 | | | | | | | |
| | | | | 6 | 6 | 3 | 9 | 27 | 13 | | 2A | 7/13 | 5 | 10 | **58** | 22 | 1 | | | | | | | | | | |
| | | | | | | | 1 | 11 | 12 | 1 | | UJ | 7L | 12 | **23** | 6 | | | | | | | | | | | |
| | | | | | | | 2 | 6 | 18 | 3 | 2 | EH | 6L | 16 | | | | | | | | | | | | | |
| | | | | | | | | 1 | 3 | 2 | | shed | 2-4 | 20 | | | | | | | | | | | | | |
| | | | | | 1 | | 2 | 5 | 35 | 26 | 714 | dp4 wr | nye/U/J | 24 | | | | | | | | | | | | | |
| **M3** | 11 | 10 | 9G | 7/8 | 5/6 | 6/7 | 5A | 3/4 | 1/2 | EJ | nye | | | nye | EJ | 1/2 | 3/4 | 5A | 6/7 | 8A | 9A | 10/ | 12 | 13 | 14 | 15 | sh | **M1** |
| | G | G | | G | G | A | | A | A | | | | | | | A | A | | A | | | 11 | A | A | A | A | | |
| | | | | | | | | | | | | E/J | | | | | | 12 | **34** | 9 | 1 | | | | | | | |
| | | | | | | | | | | | | 1/2A | | | | | | 2 | 12 | **31** | 6 | | | | | | | |
| | | | | | | | | | | | | 3/4A | | | | | | | 6 | **84** | 21 | | | | | | | |
| | | | | | | | | | 2 | 6 | | 5A | | | | | | | | 28 | **43** | | | | | | | |
| | | | | 1 | 1 | | 4 | 27 | **50** | **22** | | 6/7A | | | | | | | | 37 | **118** | | | | | | | |
| | | 0 | 3 | 30 | **21** | 1 | **13** | **31** | 22 | 3 | | 8A | | | | | | | | | **126** | | | | | | | |
| | **169** | **34** | **32** | **61** | 17 | 3 | 13 | 9 | 2 | | | 9A | | | | | | | | | **241** | 14 | 63 | 1 | 4 | 20 | 6 | |
| | 2 | | | | | | | | | | | 12A | | | | | | | | | | | | | | 2 | | |
| | 1 | | | | | | | | | | | 15A | | | | | | | | | | | | | 1 | | | |
| | | | | | | | | | | | | **M2** | | | | | | | | | | | | | | | | |

Reading from the top right quadrant working clockwise, wear stages are shown against the next-erupting tooth. The median value (highlighted and bold) is shown for the column or row of the later erupting tooth, e.g., the M1 column in the dp4/M1 quadrant. There is considerable summarising of data (for dp4 to M2, grouped stages were allotted in the proportion of the adjacent stages; for M3 and P4, because of their greater number, grouped stages were allotted equally, e.g., 9/11G a third each to 9G, 10G, 11G); nye – not yet erupted. (Totals in each quadrant may not tally because of rounding, some records do not have data for all four teeth, nye is only shown for dp4/M1 and M3/P4, and P4 is not shown in the 1st quadrant).

*Fig. 15. Relative wear of dp4, M1, M2, M3 and P4.*

| | P4 in wear M3 unworn | P4 unworn M3 in wear | M3 eruption ave. (95%) | P4 eruption ave. (95%) |
|---|---|---|---|---|
| Sheep, this study | 0 | 68 | 21 (18–24) mo | 25.5 (22–33) mo |
| Sheep, Halstead *et al*, p.c.[1] | 1[2] | 2 | | |
| Goats, D&P 1979, 1982 | all(?) | 0? | 25 (21–28) mo[3] | 22 (19–24) mo[3] |
| Goats, Noddle 1974 | 7 | 0 | | |
| Goats, Bullock & Rackham 1982 | 2 | 0 | | |
| Goats, Halstead *et al*, p.c.[1] | 9 | 0 | | |

[1] Halstead *et al* 2002, and pers. comm.; [2] P4 in wear but only half up; [3] Deniz and Payne's Table 2 (1979) and Figs. 20 and 23 (1982), females; males one month earlier; 'P2-4 erupt before M3' (1979, p.155).

*Fig. 16. Comparison of sheep with goats, where one only of P4 and M3 are in wear, and M3 and P4 eruption times.*

| Stage | Sub-divided stage | The majority of records[1] | **All records** except outliers[2] | central point | Payne 1973 estimates | Turkish goats based on D&P 1982[3] |
|---|---|---|---|---|---|---|
| A | | 0–1 mo[4] | **0 – 1 mo[4]** | 0 mo[4] | 0 – 2 mo | |
| B | | 1–3 mo | **1 – 4 mo** | 2 mo | 2 – 6 mo | – 5 mo |
| C | | 3–12 mo | **3 – 13 mo** | | 6 – 12 mo | 3 – 14 mo |
| | C1/2 | 3–5 mo | **3 – 7 mo** | 4 mo | | |
| | C3/4 | 5–8 mo | **4 – 9 mo** | 6.5 mo | | |
| | C5 | 6–9 mo | **6 – 10 mo** | 8 mo | | |
| | C6+ | 8–12 mo | **8 – 13 mo** | 10 mo | | |
| D | | 10–24 mo | **10 – 27 mo** | | 1 – 2 yrs | 11 – 30 mo |
| | D1/2 | 10–13 mo | **10 – 14 mo** | 12 mo | | |
| | D3/4 | 12–17 mo | **11 – 20 mo** | 15 mo | | |
| | D5 | 14–20 mo | **13 – 22 mo** | 17 mo | | |
| | D6+ | 18–24 mo | **14 – 27 mo** | 20 mo | | |
| E | | 20–36 mo | **19 – 54 mo** | | 2 – 3 yrs | 24 – 47 mo |
| | E1/2 | 20–30 mo | **19 – 36 mo** | 23 mo | | |
| | E3+ | 22–36 mo | **21 – 54 mo** | 30 mo | | |
| F | | 2½ – 4½ yrs | **2½ – 6 yrs** | | 3 – 4 yrs | 33 mo – 6 yrs |
| | F5/8 | 2½ – 4 yrs | **2½ – 4½ yrs** | 3 yrs | | |
| | F9/10 | 3½ – 4½ yrs | **3½ – 6 yrs** | 4 yrs | | |
| G | | 4½ – 7+ | **4 –** e.9 | | 4 – 6 yrs | 4 – 7½ yrs |
| | Ga | 4½ – e.6½ | **4 –** e.7 | 5½ yrs | | |
| | Gb | 4½ – e.8 | **4** – e.9 | e.6½ yrs | | |
| H | | 7+ | e.6 – e.11+ | e.8 | 6 – 8 yrs | 5 – 9½ yrs |
| J | | none | e.8 – e.13+ | e.10 | 8 – 10 yrs | 7 – 10+ yrs |

Figures based on: [1] the central two-thirds and [2] the 95% from the columns of Table 9; the central point is taken from visual study of the rows on Table 9. [3] using, as closely as possible, the same method as 'All records except outliers'. [4] – archaeological material at A may include pre-natal lambs; the estimated central point may most sensibly be taken as 0 months. 'e.' – estimated, see also Table 18. (Payne's late stage 'I' is re-named as 'J').

*Fig. 17. Mandible stage summary.*

| | years | 4, 4½ | 5, 5½ | 6, 6½ | 7, 7½ | 8, 8½ | 9 | 10 | 11 | 12+ |
|---|---|---|---|---|---|---|---|---|---|---|
| Sheep, this study | <H | 109 | 86 | 47 | 4 | | | | | |
| | H | | | 2H | H | | | | | |
| St. Kilda Soays | <H | 1 | 3 | 2 | 2 | 2 | 2 | | 1 | |
| Clutton-Brock *et al* 1990 | H | | | | 1H | | 1H | | 1H | |
| Shetlands | <H | 12 | 6 | 5 | | | | | | |
| Davis 1996, 2000 | H or J | | | 4H 1J | | | | | | |
| Museum study sheep | <H | 17 | 6 | 5 | | | | | | |
| Moran & O'Connor 1994, p.c. | H or J | 2H | 1H | 7H | | 2J | 1H 3J | | | |
| Butser Shetland ram (?9 or 10 yrs) | | | | | | | 1H | | | |
| Awassi sheep, Weinreb/Sharav 1964 | | | | | | | | | 1J | |
| Suffolk cross ewe, Griffith, p.c. | | | | | | | | | | 1J (16yrs) |

Grant's stage 'h' is taken as equivalent to 9A (or 11G), for defining G, H and J.

*Fig. 18. Erasure of the infundibula in comparative sources; known-age sources, stages H and J.*

| | | | | G | H | J | ratio (%) | F M1>9A | Ga | Gb |
|---|---|---|---|---|---|---|---|---|---|---|
| Sheep, this study | (no old sheep) | UK | Modern | 152 | 3 | 0 | 98: 02: 00 | 4 +* | 57 | 95 +* |
| sheep(goat) | Grant 1982, Table 3 | UK | RB-med. | 213 | 62 | 12 | 74: 22: 04 | 36 | 31 | 182 |
| sheep(goat) | Dobney *et al* 1996, Table 33 | UK | Med. | 35 | 6 | 3 | 80: 14: 07 | | | |
| sheep/goat | Payne 1973, Fig. 12 | Turkey | Hell.-med. | 15 | 7 | 6 | 54: 25: 21 | | | |
| sheep | Payne 1973, Fig. 14 | Turkey | Modern | 5 | 5 | 1 | 46: 46: 08 | | | |
| sheep | Halstead, p.c. | Greece[1] | Late neo. | 72 | 53 | 22 | 49: 36: 15 | 11 | 2 | 46 |
| goat | Halstead, p.c. | Greece[1] | Late neo. | 31 | 6 | 2 | 79: 15: 05 | 12 | 0 | 21 |
| sheep + goat | Halstead, p.c.[2] | Greece[1] | Late neo. | 212 | 122 | 29 | 58: 34: 08 | | | |

* - 4 definites, plus 9 at F/G, see text, 'Sheep aged two to seven years old'; [1]- Makrigialos, N. Greece (phase I early Late Neolithic); [2] including grouped jaws (e.g. G/H), assigned proportionately.

*Fig. 19. Erasure of the infundibula in other sources; the ratio of G, H and J, and erasure of M1.*

| **Age in years** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **19** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Year of birth** | **2002** | **2001** | **2000** | **1999** | **1998** | **1997** | **1996** | **1995** | **1994** | **1993** | **1992** | **1991** | **1990** | **1989** | **1988** | **1987** | **1986** | **1984** | |
| Females | 2109 | 2178 | 2046 | 1799 | 1841 | 1505 | 1427 | 1326 | 1193 | 867 | 162 | 76 | 61 | 29 | 16 | 2 | 1 | 1 | 16639 |
| Males | 1518 | 909 | 349 | 213 | 242 | 207 | 192 | 181 | 174 | 163 | 6 | 3 | 1 | | 1 | 1 | | | 4160 |
| Total | 3627 | 3087 | 2395 | 2012 | 2083 | 1712 | 1619 | 1507 | 1367 | 1030 | 168 | 79 | 62 | 29 | 17 | 3 | 1 | 1 | 20799 |

Combined breeds: Boreray, Castlemilk Moorit, Manx Loghtan, Norfolk Horn, North Ronaldsay, Portland, Soay and Whitefaced Woodland; data from RBST; E. Henson, Grassroots System, pers. comm. (information from all breeders who made a return in 2002).

*Fig. 20. The age of live registered Rare Breed sheep, in the UK, in January 2003.*

*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 179–188*

# 11. Determining the Age of Death of Proboscids and Rhinocerotids from Dental Attrition

*S. Louguet*

*Archaeological deposits producing a great deal of Proboscidean and Rhinocerotidae remains with lithic assemblages from Hominid occupations are common in Europe from the Pleistocene era. The difficulty when examining such bone assemblages is to recognize whether these deposits are the result of hunting or scavenging. Consequently, it is useful to identify the age of death of each individual from the fossil populations concerned. The dental attrition method represents the preliminary stage of reconstructing mortality profiles, which, included in a global study, will allow us to interpret them, either in terms of natural mortality, of catastrophic massive mortality, or of selective hunting.*

*In this work, I will present the dental attrition method applicable to Proboscids and Rhinocerotids described from some attrition sequences I define. With this aim in view, I draw some wear patterns corresponding to the different stages in the life of a tooth in order to attribute to each one an attrition stage, according to its abrasive surface. Afterwards, the method will be applied to populations of large herbivores, from two important French sites, and their mortality profile will be interpreted. These are the Proboscids from Hanhoffen (Bas-Rhin, France) and the Rhinocerotids from Biache-Saint-Vaast (Pas-de-Calais, France).*

## Introduction

Archaeological sites from the Pleistocene era producing many Proboscidean and Rhinocerotidae remains in association with lithic vestiges from Hominid occupations are common in Europe. Taphonomic and zooarchaeological studies of these remains inform us about the animals' treatment. However, it is not so easy to determine the acquisition methods of these large herbivores by prehistoric humans. The difficulty of the analysis of such bone assemblages is to know whether these deposits are the result of hunting or scavenging from naturally dead animals by Hominids, or victims of other predators. Consequently, it is also useful to identify the age of death of each individual from the fossil populations concerned to contribute to the interpretation. This identification is done mainly by using the dental attrition method. In fact, a single tooth may provide a great deal of information about the animal, such as its species and its degree of evolution but also its age of death. Moreover, the tooth structure and especially its composition provide a better preservation than a bone, which is why teeth are usually ideal to work with.

In this study, the dental attrition method is applied to Proboscids and Rhinocerotids, very large herbivores whose hunting by prehistoric people is still the inspiration for extensive discussion and debate. First, I am going to present the dental attrition method as applied to Proboscids and Rhinocerotids described using some attrition sequences that I define. The method will be applied to two populations of large herbivores from two important French sites, and their mortality profile will be interpreted from the results. These are the Proboscids from Hanhoffen (Bas-Rhin, France) and the Rhinocerotids from Biache-Saint-Vaast (Pas-de-Calais, France).

## The Dental Attrition Method: Presentation and Interest

### *Proboscids*

*Proboscidean dentition*

Proboscids, mammoths and elephants, have only six cheek teeth per half-jaw which follow each other all through their life. One molar is constituted of a series of transversal plates held together by cement. Each plate is composed of a thin ivory fold covered with an enamel layer (Fig. 1). Among the cheek teeth, there are three milk teeth, D1, D2, D3, and three permanent teeth, M1, M2, and M3. In fact, the substitution mode of Elephantidae cheek teeth is unusual because it occurs in a horizontal manner, unlike the majority of mammals where it occurs vertically. Therefore, only one or even two teeth function at the same time (Fig. 2). Consequently, little by little a tooth wears horizontally, that is, perpendicularly to the lamellas, up to its fall when it is almost totally worn. Then, the next larger tooth, which has pushed behind the worn tooth, replaces it. This succession comes to an end only when the last tooth is completely worn; therefore the animal is disabled from eating, and consequently dies of hunger.

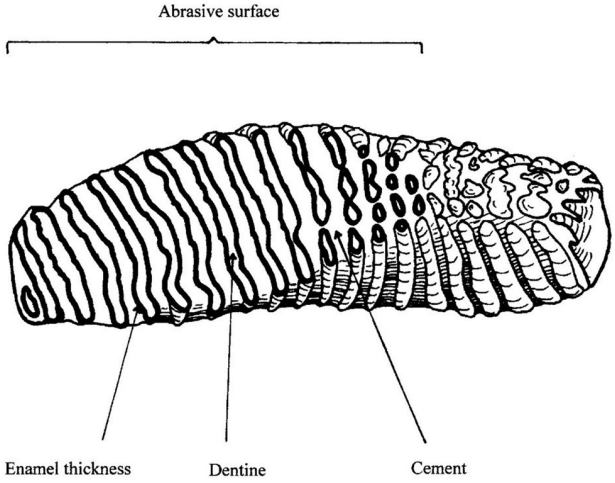


*Fig. 1. Composition and structure of a mammoth tooth, in occlusal view.*

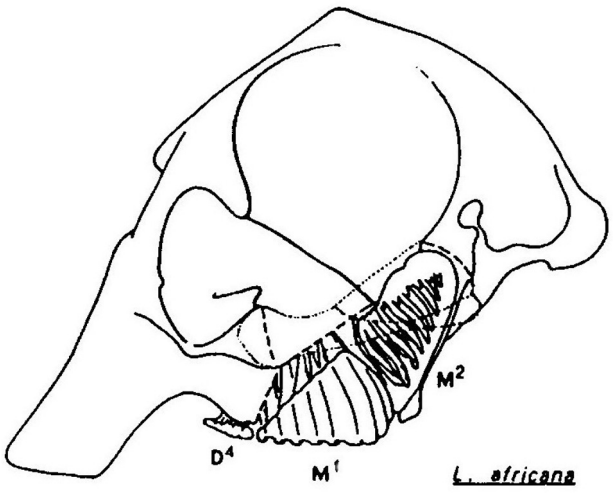


*Fig. 2. Layout of Elephantid cheek teeth, according to Beden, (1979).*

### *Age groups*

Several methods were proposed for appraising the attrition of Proboscidean teeth, but the method conceived by Beden in 1979 on the lower teeth seems the most appropriate. The attrition levels of Elephantidae cheek teeth (Fig. 3), consider the attrition condition of the plates on the whole, but also their gradient, so that even a fragment of tooth can be situated in the model.

Beden took care to number the different attrition levels from the new tooth, not worn (A level) to the totally worn one 100% abraded (D4 level), including the levels of increase of plates in function and the levels corresponding to the progressive destruction of them. Beden applied this model to lower teeth, but later studies have successfully applied it to the upper dentition (Louguet 2000).

So in order to elaborate the mortality profile of an Elephantidae population, it is necessary to define some age groups by taking into account the position of each tooth in the cheek teeth series, as well as its worn level. In fact, only the position of the tooth in the series is not a sufficient parameter because it produces too approximate an age interval.

Finally, we correlate the whole with the model of present-day elephants using Haynes (1991), as it is presented in Fig. 4. In fact, African and Asian elephants have a dental formula similar to those of mammoths and straight tusk elephants (i 0/0, c 0/0, p 3–4/3–4, m 3/3, according to Guérin (1980)). Consequently, the age intervals obtained from a modern species of elephant seem to represent a relatively limited margin of error. On the basis of this information and the numerous age groups established by Laws in 1966, seven main age intervals were defined. These allow us to elaborate relatively precise mortality profiles.

### *Interpretation of mortality profile among Proboscids (according to Haynes)*

Once a histogram showing the mortality profile is complete, we can try to interpret it and set up hypotheses about the causes of the death of the animals. With this aim in view, we compare each profile with the models established by Haynes (1987) on present elephant populations. Notable is that the first three age groups defined by us constitute only one group in Haynes, the interval

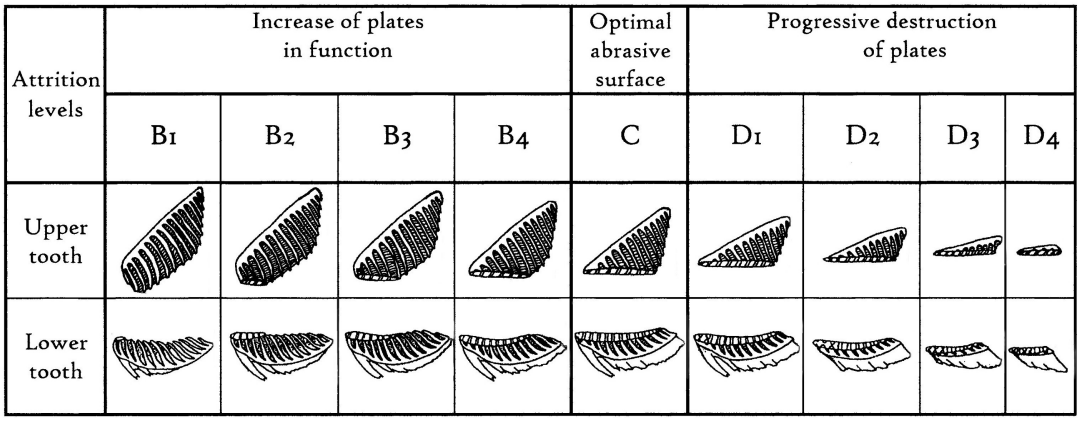


*Fig. 3. Attrition levels of Elephantid cheek teeth, according to Beden, (1979) (lower teeth) and Louguet, 2000 (upper teeth).*

| ELEPHANTIDS DENTITION | | AGE ESTIMATION |
|---|---|---|
| **Teeth** (Laws 1966) | **Attrition levels** (Louguet 2000) | According to African Elephant (Laws 1966 ; Haynes 1991) |
| D2 | All levels | < 2 years |
| D3 | A to C | |
| D4 | A | |
| D3 | D | ~ 2 to 5 years |
| D4 | B to C | |
| M1 | A | |
| D4 | C to D3 | ~ 5 to 12 years |
| M1 | A to B3 | |
| M2 | (A) | |
| D4 | D4 | ~ 12 to 22 years |
| M1 | C to D2 | |
| M2 | A to B2 | |
| M1 | D3 to D4 | ~ 22 to 35 years |
| M2 | B3 to D2 | |
| M3 | A to B2 | |
| M2 | D3 to D4 | ~ 35 to 48 years |
| M3 | B3 to C | |
| M3 | D | ~ 48 to 60 years |

*Fig. 4. Age intervals of Proboscidea corresponding to dental attrition levels.*

from the birth to the age of eleven years. Below are the four main types of death profiles and their characteristics according to Haynes (1987) (Fig. 5):

- Type A: non-selective mortality in stable populations.
- Type B: selective mortality affecting mixed herds.
- Type C: non-selective mortality affecting declining populations.
- Type D: varied causes.

### *Rhinocerotids*

*Rhinoceros dentition*

The dental attrition method becomes more complex for rhinoceros that can show six teeth per half-jaw simultaneously, but the wear level of each tooth differs according to its position in the dental series. In fact, the three species of Pleistocene Rhinocerotidae considered here have per half-jaw four milk teeth, D1, D2, D3 and D4, progressively replaced by six permanent teeth, three premolars P2, P3 and P4, and three molars, M1, M2 and M3. Then, the dentition appears in a particular order which is approximately the following, according to Guérin (1980):

- Eruption of D3, then D2, D4 and finally D1
- Eruption of M1
- Fall of D2 and eruption of P2
- Fall of D3 and eruption of P3
- Eruption of M2
- Fall of D4 and eruption of P4
- Eruption of M3
- (Fall of D1 variable and not necessary)

*Age groups*

The dental attrition method primarily consists of drawing some wear patterns corresponding to the different stages in the life of each tooth, as it is presented in Figs 6 –10.

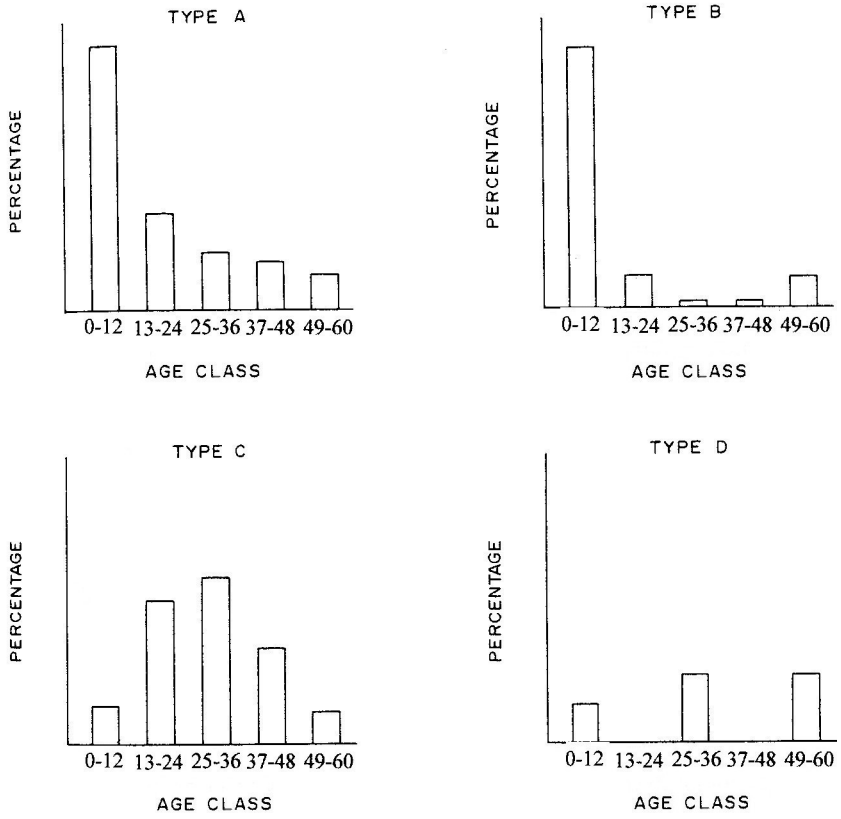


*Fig. 5. The four main types of age profiles found for living and extinct Proboscidean bone assemblages, according to Haynes, 1987.*

Thus, these drawings, represent several horizontal sections of each tooth and contribute to defining our attrition stages.

Tables were established according to the study of numerous dental series from rhinoceros remains (*Dicerorhinus hemitoechus*) from the archaeological collection of Biache-Saint-Vaast (Pas-de-Calais, France). The first table (Fig. 11) corresponds to the model of the upper dental series, and the second (Fig. 12) to that of the lower ones. Thus, eight age groups can be defined. Approximate calendar ages can be attributed to these thanks to the study of black rhinoceros by Goddard (1970) and its interpretation by Germonpré (1989).

Moreover, Pleistocene rhinoceros teeth can be entered in this model because even if the biometry or the morphology of the teeth differ, the order of the dental eruption remains the same for all species: *Dicerorhinus hemitoechus*, *Dicerorhinus mercki* or *Coelodonta antiquitatis.*

Consequently, once the combination of the different attrition stages of each tooth have been made for the dental series, it is possible to calculate the age interval to which the animal belonged at its time of death. This interpretation will be more or less restricted by the number of teeth from the dental series we have. In fact, even an isolated tooth can be placed in the model when compared to the attrition table, but in this case, the age interval obtained will be perhaps less precise than it would be with two teeth or more from a same series. It is particularly the case with cheek teeth whose age of eruption is very variable, and this constitutes the main limit of this method. It is common to obtain intermediary age intervals when two age groups are possible. When this happens, we may redistribute the value of the intermediary interval between the two groups in a proportionate manner. The histogram illustrating the rhinoceros mortality profile remains composed of eight age groups.

### *Interpretation of mortality profile among Rhinocerotids*

The different types of mortality profiles presented previously were defined by Haynes according to the study of modern elephants. The lifeways of the rhinoceros differ from that of elephant; evidence of herding behaviour is not found in the case of rhinoceros, for example. Nevertheless, we may meet these types of mortality profiles among rhinoceros populations, and consequently, the

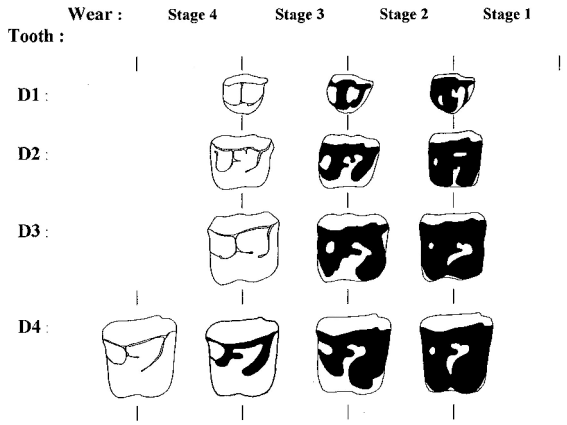


*Fig. 6. Different stages of wear of* Dicerorhinus hemitoechus *upper milk dentition.*

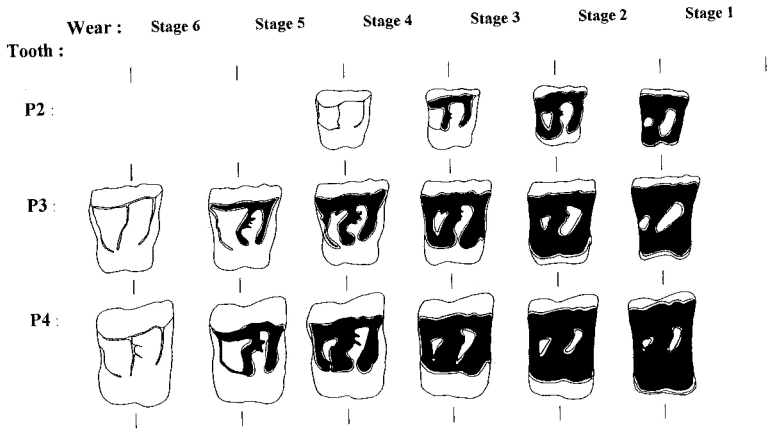


*Fig. 7. Different stages of wear of* Dicerorhinus hemitoechus *upper premolars.*

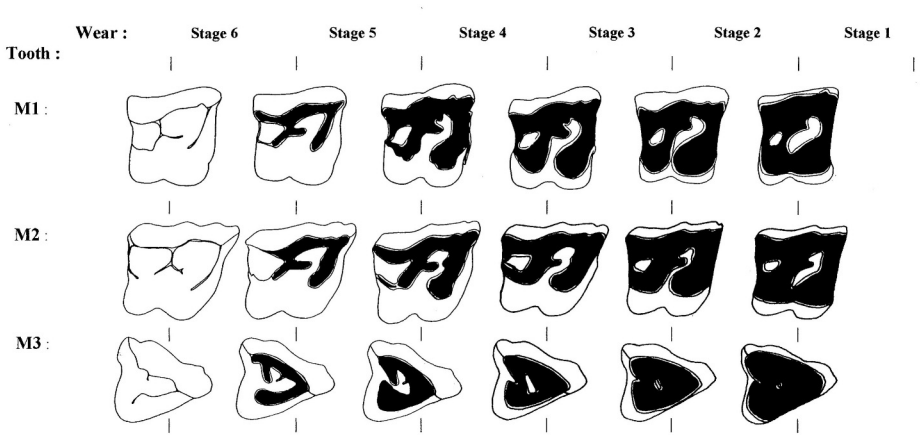


*Fig. 8. Different stages of wear of* Dicerorhinus hemitoechus *upper molars.*

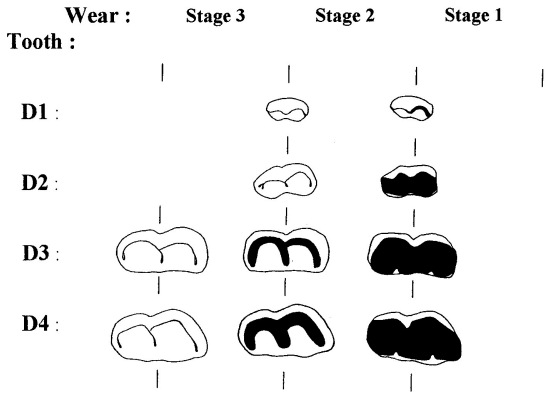


*Fig. 9. Different stages of wear of* Dicerorhinus hemitoechus *lower milk dentition.*

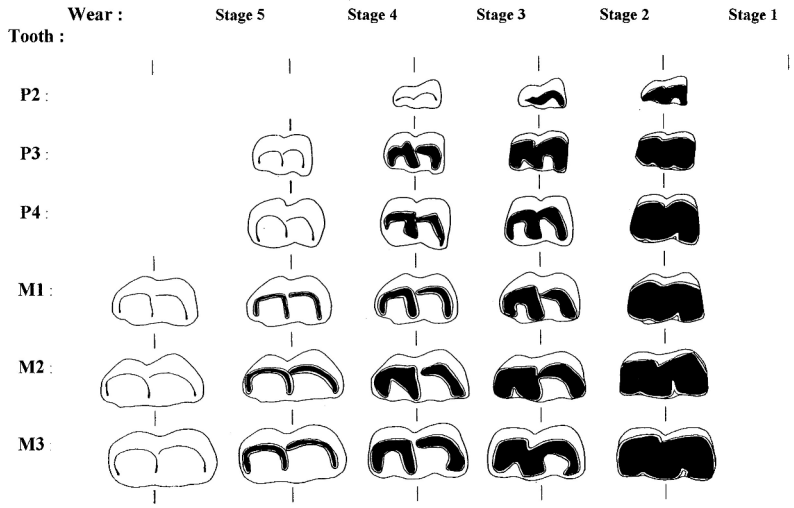


*Fig. 10. Different stages of wear of* Dicerorhinus hemitoechus *lower permanent dentition.*

models defined by Haynes are able to contribute to their interpretation in general outlines.

## Application of the Method to Two Large Herbivores Populations and Results

### *Application of the method to the Proboscidea from Hanhoffen*

*Presentation of the site of Hanhoffen (Bas-Rhin, France)*

The site of Hanhoffen is located on a quaternary terrace of the Rhine Valley in Alsace in Eastern France, approximately 30 km from Strasbourg (Fig. 13). The remains come from the private collection of Georges Rocques; the collection is now stored at the Prehistoric Museum of Arras (France).

The gravel pits of Hanhoffen yielded a lot of middle and upper Pleistocene Elephantidae remains (almost 50% of the bones), and other big herbivores which were excavated by workers. However, no human remains or evidence of industry were found there. Unfortunately, the extraction conditions did not allow us to get any stratigraphic information of the bones assemblages.

Finally, the remains seem to have settled relatively quickly, after a short transport by a river. In fact, the biggest or heaviest pieces dominate the whole assemblage while the lightest elements such as ribs, metapodia, or vertebrae, are almost absent. A possible selection of the most beautiful elements and the biggest ones by workers seems to be minor. In fact, among other species (cervids, equids, etc.), many small pieces (such as teeth) were collected by excavators. So we can consider that the dominance of large bones results essentially from river transport.

| Upper milk dentition | | | | Upper permanent dentition | | | | | | Group | Age |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **D1** | **D2** | **D3** | **D4** | **P2** | **P3** | **P4** | **M1** | **M2** | **M3** | | **(Goddard 1970)** |
| 3 | 3 | 3 | 4/3 | | | | | | | I | 0 - 1 year |
| 2/1 | 2/1 | 2/1 | 3/2 | | | | 6 | | | II | 1,5 - 3 years |
| (1) | (1) | (1) | 2/1 | 4 | 6 | (6) | 6/5 | 6 | | III | 4 - 5 years |
| ? | | | | 4/3 | 5/4 | 6/5 | 5/4 | 6/5 | 6 | IV | 6 - 7 years |
| ? | | | | 3/2 | 4/3 | 4/3 | 4/3 | 5/4 | 6/5 | V | 8 - 9 years |
| ? | | | | 2/1 | 2/1 | 3/2 | 3/2 | 3/2 | 4/3 | VI | 10 - 12 years |
| ? | | | | (1) | (1) | 1 | 2/1 | 2 | 2/1 | VII | 14 - 21 years |
| ? | | | | ? | ? | ? | ? | 1 | 1 | VIII | 25 - 40 years |

*Fig. 11. Age groups of Pleistocene Rhinoceros based on the stages of wear of their upper dentition. Numerals correspond to attrition stages of each tooth. A numeral in parentheses means that the presence of the tooth is not obligatory yet. "?" means that the tooth is probably fallen.*

| Lower milk dentition | | | | Lower permanent dentition | | | | | | Group | Age |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **D1** | **D2** | **D3** | **D4** | **P2** | **P3** | **P4** | **M1** | **M2** | **M3** | | **(Goddard 1970)** |
| 2 | 2 | 3/2 | 3 | | | | | | | I | 0 - 1 year |
| 2/1 | 2/1 | 2/1 | 2/1 | | | | 5 | | | II | 1,5 - 3 years |
| (1) | (1) | (1) | 1 | 3 | 4 | (4) | 5/4 | 5 | | III | 4 - 5 years |
| ? | | | | 3/2 | 4/3 | 4 | 4/3 | 4/3 | 5/4 | IV | 6 - 7 years |
| ? | | | | 3/2 | 3/2 | 4/3 | 3/2 | 3/2 | 4/3 | V | 8 - 9 years |
| ? | | | | 2/1 | 3/1 | 3/2 | 1/2 | 3/1 | 3/2 | VI | 10 - 12 years |
| ? | | | | (1) | (1) | 2/1 | 1 | 2/1 | 2/1 | VII | 14 - 21 years |
| ? | | | | ? | ? | ? | ? | 1 | 1 | VIII | 25 - 40 years |

*Fig. 12. Age groups of Pleistocene Rhinoceros based on the stages of wear of their lower dentition. Numerals correspond to attrition stages of each tooth. A numeral in parentheses means that the presence of the tooth is not obligatory yet. "?" means that the tooth is probably fallen.*

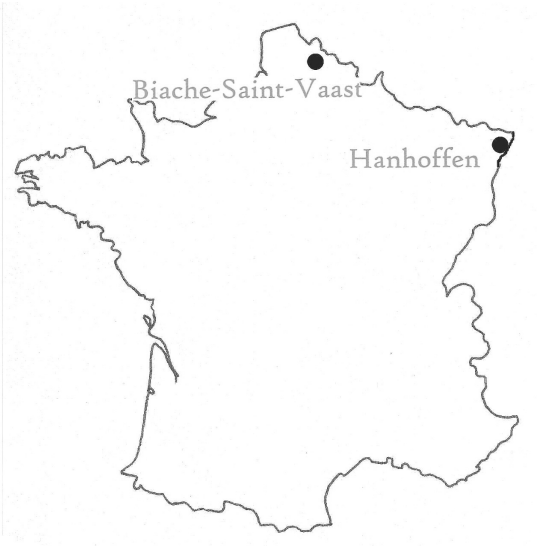


*Fig. 13. Map showing locations of the two Pleistocene sites in France mentioned in the text.*

*Mortality profile of the Proboscidea from Hanhoffen*

The woolly mammoth is the main species represented in Hanhoffen with a minimum number of 99 individuals. The paleontological study of *Mammuthus primigenius* from Hanhoffen was carried out on 421 cheek teeth.

The mortality profile obtained by the dental attrition method presents a dominant group which corresponds to 22–35 year old adults with nearly 40% of the total dead population, followed by the group of the young adults, between 12 and 22 years old with a representation of almost 25% of the sample (Fig. 14).

This profile does not show a significant percentage of very young individuals, as would be the case in models such as selective hunting or a catastrophic massive death event encountered by a population in extension. Also, the oldest age interval is not dominant, which means that the whole population of Elephantidae represented in the sample did not die of old age, every age group being represented on the site.

The mortality profile obtained from representatives of

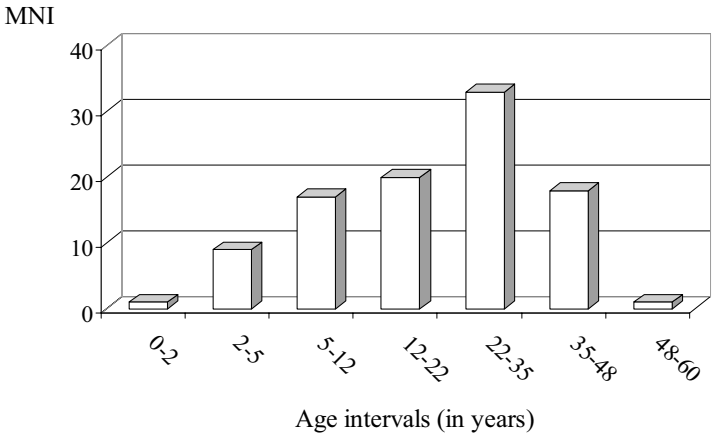


*Fig. 14. Mortality profile of the* Mammuthus primigenius *from Hanhoffen (Bas-Rhin, France) based on dental remains.*

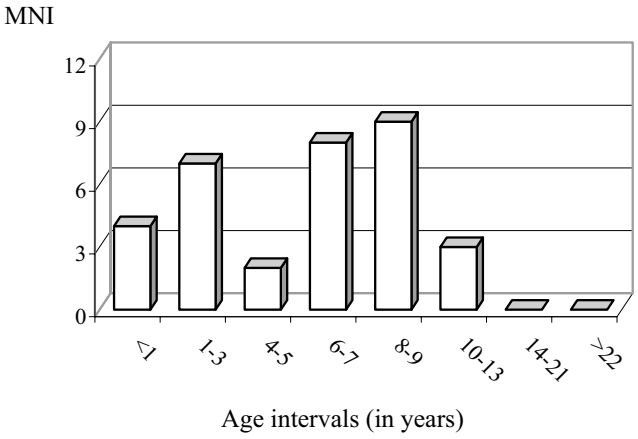


*Fig. 15. Mortality profile of* Dicerorhinus hemitoechus *from Biache-Saint-Vaast (Pas-de-Calais, France) based on upper dentition.*

*Mammuthus primigenius* would correspond to a non-selective mortality affecting a declining population, similar to the "Type C" model defined by Haynes (1987).

*Interpretation of the mortality profile*

The Proboscidea here have probably not been the victims of a single event; death could result from several factors. Among them, the most probable are the diseases, accidents (falling, drowning, etc.), malnutrition (worsened by the drought), old age, and often predatorial interventions (others than Hominids). In the case of Hanhoffen, no evidence of hunting exists on the bone remains. A few gnaw marks and bites attributable to animal predators observed on the bones probably result from scavenging.

Finally, the taphonomic analysis of bones, carried out by Auguste P. (UPRESA 8018, CNRS), shows that no marks of human activity (such as cuts) are present on the bones remains. This promotes the hypothesis of a non-selective mortality of natural origin.

## Application of the method to the rhinoceros from Biache-Saint-Vaast

### *Presentation of Biache-Saint-Vaast (Pas-de-Calais, France)*

The Biache-Saint-Vaast site (Fig. 13), located in Pas-de-Calais (Northern France), would be attributable to the seventh isotopic stage of the Saalien interglacial period. The fluvial deposits of the terrace delivered, in addition to Neanderthal cranial remains, a great deal of herbivore bones associated with a Mousterian industry (Tuffreau

and Sommé 1988). Among the 11 archaeological levels, Level IIa is the richest. It seems correspond to several human occupations. Moreover, the good preservation of the bone surfaces indicates a rapid burying of the dead animals. Three species dominated the fauna: aurochs (*Bos primigenius*), brown bear (*Ursus arctos*) and rhinoceros (*Dicerorhinus hemitoechus*). Their bones show some marks of cuts (20 to 30 % of the bones), revealing that their flesh was removed by people. However, gnaw marks produced by carnivores are rare (less than 5%). Finally, many bones were broken by Hominids (Auguste 1995a).

*Mortality profile of the rhinoceros from the IIa level of Biache*

Two species of Rhinocerotidae are represented in Level IIa of Biache-Saint-Vaast, but the prairie rhinoceros (*Dicerorhinus hemitoechus*) dominates distinctly over the Merck rhinoceros (*Dicerorhinus mercki*), with a minimum number of 41 individuals against 12 for the second species. Thus, only the prairie rhinoceros from Level IIa was considered for the study. A death profile was produced from the bony remains by Auguste (1995b). A more detailed study of the dentition, however, allowed the definition of a more significant number of age groups, and consequently a more exact age profile. The histogram, Fig. 15, was produced showing 329 upper teeth, of which 41 dental series include a minimum of 2 teeth, and 63 isolate teeth.

The mortality profile obtained by the rhinoceros dental attrition does not present any old individuals which could have died of old age in natural conditions; these adults are absent in the sample. On the other hand, young animals between 6 and 9 years are the most represented, with more than 50% of the total.

*Interpretation of the mortality profile*

The small representation of the individuals under 5 years, compared with the more significant group of the 6–9 year olds can be explained if we consider the ontogeny of modern rhinoceros. The young rhinoceros stays under its mother's protection for a minimum of 2 years, and often until 5 years. And even while on its own thereafter, its size will still increase progressively until the age of nine. This explains a low infant mortality. The more important peak of death, observable in the profile, coincides precisely with the moment when the young individuals leave their mother and have not yet reached adulthood, the moment when they are the most vulnerable. Consequently, the hypothesis of hunting cannot to be ruled out. The site, located in a fluvial context, seems to have been associated with a large zone of marshlands that must have offered an easy trap for the larger herbivores. Moreover, we know that rhinoceroses are animals with regular habits, and whose biotope is always associated with the presence of a watering hole that they visit regularly. Here, the animals must have come to the bank of the Scarpe river in order to drink.

Finally, on the basis of the spatial distribution of the bones, an *in situ* killing site may be considered. The height and mass of a rhinoceros do not allow for easy transport. So the hunters probably butchered them at the kill site, as is suggested by the numerous bone fragments which seem to have been the result of anthropogenic fractures. The common rhinoceros bones concerned are humerus and tibiae, bones that give the most bone marrow. A hunting selection of various game seems to have been carried out because only three species are dominantly represented at this level while the biotope of Level IIa of Biache-Saint-Vaast is very diversified, representing almost 20 different species.

## Conclusion

Large herbivore remains often ignite discussions concerning the interpretation of their causes of death. Animal teeth, which preserve better than bone, are interesting to examine in this respect as they can inform us about the age of death of an individual. As we have seen for Proboscidea, it is fairly easy to identify an age interval using a single tooth. The method is more complex for rhinoceros because of the increased number of teeth in a series. In fact in both cases, the age interval will be more or less restricted according to the number of teeth from the dental series available for study.

This attrition method represents the preliminary stage of reconstructing mortality profiles, which, included in a global study, will allow us to interpret them in terms of natural mortality, catastrophic massive mortality, or selective hunting.

*Acknowledgements*

I would like to thank the following people for allowing me to study their material: J.-L. Marcy (curator of the Prehistoric Departmental Museum of Arras where the bones are stored), A. Tuffreau (professor and researcher) and P. Auguste (researcher), for the material of the exceptional site of Biache-Saint-Vaast, and also for the material of Hanhoffen collected by G. Roques. I wish to thank the Institute for Aegean Prehistory for the generous grant which allowed me to attend the meeting in Durham.

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*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 189–203*

# 12. Tooth Wear in Wild Boar (*Sus scrofa*)

*O. Magnell*

*In order to study the limitations and possibilities of age estimation based on tooth wear of skeletal remains from wild boar, 315 mandibles from five different populations of wild boar from Poland, Germany and Sweden were analysed. Asymmetric tooth wear between the right and left mandibles was found to be rare and no systematic difference in tooth wear between males and females (less than 36 months) could be proven. The rate of tooth wear seems to vary between different populations of wild boar. The largest difference was found between wild boar kept in enclosures and four populations of free-ranging animals that showed relatively small difference in tooth wear of individuals younger than 36 months. The analysis reveals a strong correlation between age and mandible wear stages (MWS)/ tooth wear stages (TWS) and indicates that tooth wear can be useful in age estimation of mandibles or loose teeth of wild boar. However, the individual variation of tooth wear is relatively large and increases with age, which implies that long lasting TWS and MWS can only be restricted to broad age groups.*

## Introduction

Tooth wear, together with eruption, is one of the most frequently used and reliable methods of ageing animal remains from archaeological sites. The tooth eruption of wild boar and domestic pig has been investigated in several studies (Habermehl 1961; Briedermann 1967; Koslo and Nikitenko 1967; Matschke 1967; Silver 1969; Hayashi *et al.* 1977; Bull and Payne 1982; Boitani and Mattei 1991; Genov *et al*. 1991; Clarke *et al.* 1992; Bridault *et al*. 2000). The sequence of the eruption of the teeth is consistent in these studies. The ages at eruption of teeth in wild boar given in these different studies are, to a great extent, in accordance, while the eruption in domestic pig is a few months earlier, especially in the third molar (Bull and Payne 1982, 56; Hillson 1986, 208).

In comparison with tooth eruption, the relationship between age and tooth wear in wild boar is much less studied. Methodological studies of tooth wear in wild boar and domestic pig are relatively few (Koslo and Nikitenko 1967; Grant 1982; Rolett and Chiu 1994). None of the studies includes analysis of modern reference collections with known age or presentation of quantitative wear data, making it impossible to evaluate the relationship between tooth wear and age in wild boar in the same way as have been done in studies of other species, such as red deer, domestic sheep and goat (Deniz and Payne 1982; Brown and Chapman 1991; Moran and O´Connor 1994). It is therefore important to establish a technique that would allow one to convert tooth wear scores into age classes in order to interpret age structures and how they relate to the life history characteristics of the animal. Only when this relationship has been analysed, will it be possible to draw conclusions about hunting or animal management in the past.

Ageing by tooth wear is useful since it can be used on mature dentition with erupted permanent teeth. Tooth wear can also be used for ageing loose teeth, while tooth eruption only can be used on more or less complete mandibles or maxillae. In archaeological materials, complete mandibles of wild boar are rare, while large quantities of loose teeth and fragmented mandibles often

are recovered, especially if the excavated soil has been sieved. Including loose teeth in analysis of age structures in a sample is also important from a taphonomic point of view, as mandibles of juvenile animals are less frequently preserved than those of adult animals. Several studies show that mandibles of juveniles are more sensitive to density-mediated bone destruction than mandibles of adult animals (Binford and Bertram 1977; Munson 2000). However, relatively large numbers of teeth can often be recovered when the soil has been sieved. The inclusion of loose teeth allows a more complete analysis of age structures in archaeological samples.

A problem with using tooth wear in ageing is that the rate of attrition is affected by different factors, such as variation in tooth eruption, coarseness of food and amount of abrasive particles in the diet (Hillson 1986, 184–185). In this study, tooth wear in mandibles of wild boar in modern collections will be analysed in order to investigate the limitations, but also the possibilities in using tooth wear for the ageing of mandibles and loose teeth of wild boar. The variation of tooth wear has been studied on different levels, from the individual dentition to within and between populations from various areas in Northern Europe.

In a study of tooth wear in American elk, it was noticed that the wear on the right and left sides of the mandibles in some individuals was strikingly different (Quimby and Gaab 1957, 435–436). Bones recovered from archaeological sites are most often fragmented and mandibles are frequently broken in a right and left part. The differences in tooth wear between the right and left tooth rows have been analysed in order to investigate to what degree asymmetric wear could be a source of error in ageing of wild boar.

Deniz and Payne (1982) showed that the rate of tooth wear differs between males and females in mandibular dentitions of Turkish Angora goats. The tooth wear was similar between the sexes during the first year, but by 30 months of age, tooth wear in males was three months ahead of that in females (Deniz and Payne 1982, 181–187). However, in a study of the correlation between dental crown height and age in red deer, the regression for males and females was very similar and it was concluded that the rate of attrition varies insignificantly between the sexes (Klein *et al.* 1981, 11). An attempt here has been made to investigate if the rate of tooth wear varies between males and females in wild boar.

It is often asserted that rates of tooth wear may differ between different populations of animals (Grant 1978; Hillson 1986, 184). There is, however, relatively few studies investigating this problem. Variation in the rate of attrition between different populations has been shown for domestic sheep and goat (Healy and Ludwig 1965; Deniz & Payne 1982). The problem with inter-population differences in the rate of attrition is considered to be greater in domesticated animals in comparison with wild animals (Hillson 1986, 184; Brown and Chapman 1991, 535). In red deer and fallow deer, there seems to be lower variation in wear between different populations (Chaplin and White 1969, 131; Lowe 1967, 148–149). In this study, the variability in tooth wear between five populations of wild boar from different areas and environments will be analysed.

## Material

A total of 315 mandibles of wild boar in different age groups from five populations in Poland, Germany and Sweden were studied. The samples vary in size and also in distribution between different age groups (Fig. 1).

A sample of 68 mandibles of wild boar that were killed or found dead from 1956–1982 in the Bialowieza Primeval Forest (BPF), Poland, was studied. The mandibles are not from individuals of known age, but the dates of death are known. The Bialowieza Primeval Forest is famous for being one of the best preserved temperate forest ecosystems in Europe. The forest is dominated by deciduous trees, mainly oak (*Quercus robur*), hornbeam (*Carpinus betulus*), lime (*Tilia cordata*) and maple (*Acer platanoides*) (Jedrzejewska *et al.* 1994, 665–668).

A further 53 mandibles were obtained from the breeding reserves of the Mammal Research Institute in Bialowieza (BBR) during 1961–1970. Forty-four of the mandibles originate from crossbreeding experiments between wild boar and domestic pig. The animals were kept in enclosed areas with deciduous tree stands and were given supplementary food. It is not ideal to have crossbreeds in a study of wild boar, but the sample is useful since all mandibles are from individuals of known age.

From Kampinos National Park (KNP) near Warsaw, Poland, 29 mandibles from wild boar killed in 1963–1970 were studied. The age of 16 mandibles from individuals captured and ear-tagged as piglets are known. The dates of slaughter of the other 13 mandibles are known. The area of Kampinos National Park is forested with mixed woods, dominated by hornbeam and extensive marshlands (Andrzejewski and Jezierski 1978).

All the mandibles from the three Polish wild boar populations were studied in the collections of the Mammal Research Institute in Bialowieza. The largest sample in the study consists of 143 mandibles from wild boar shot during 1960–1993 in Schleswig-Holstein (S-H), northern Germany. The date of slaughter is known, but not the absolute age. The wild boar originate from an area dominated by an agricultural landscape mixed with broadleaf forests covering about 10% of the area (Ministerium für Umwelt, Natur und Forsten des Landes Schleswig-Holstein 2001). The mandibles belong to the collections of *Institut für Haustierkunde*, University of Kiel.

The last sample consists of 22 mandibles from wild boar killed between 1999–2002 in the north-eastern part

| Age | Bialowieza P.F. | | | | Bialowieza B.R. | | | | Kampinos N.P. | | | | Schleswig-Holstein | | | | Scania | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (months) | M | F | u | Totals | M | F | u | Totals | M | F | u | Totals | M | F | u | Totals | M | F | u | Totals |
| 0–2 | 1 | 1 | | 2 | 12 | | | 12 | | | | | | | | | | | | |
| 5–6 | | 1 | 1 | 2 | 3 | 3 | | 6 | | | | | 1 | | 6 | 7 | | | | |
| 7–8 | 1 | 1 | 2 | 4 | 2 | | | 2 | 3 | 3 | | 6 | 1 | 1 | 10 | 12 | | | 2 | 2 |
| 9–11 | 8 | 6 | 6 | 20 | 5 | 4 | | 9 | 3 | 4 | | 7 | 15 | 4 | 21 | 40 | 4 | | 1 | 5 |
| 12–13 | 3 | | 2 | 5 | 1 | 1 | | 2 | 3 | | | 3 | 17 | 8 | 14 | 39 | 5 | | | 5 |
| 14–18 | 3 | 3 | | 6 | 3 | 4 | | 7 | 2 | 2 | | 4 | 7 | 11 | | 18 | 1 | 3 | 1 | 5 |
| 19–24 | 4 | 1 | | 5 | 2 | 5 | | 7 | 2 | 2 | | 4 | 1 | 12 | | 13 | 1 | 3 | | 4 |
| 25–36 | 4 | 4 | | 8 | 2 | 1 | | 5 | | | | | | 7 | | 7 | | 1 | | 1 |
| >36 | 5 | 11 | | 16 | 2 | 1 | | 3 | 2 | 3 | | 5 | | 7 | | 7 | | | | |
| Total | | | | 68 | | | | 53 | | | | 29 | | | | 143 | | | | 22 |

*Fig. 1. Samples of mandibles from five different populations used to study tooth wear in wild boar. M= males, F= females, u= sex unknown, P.F.= Primeval Forest, B.R. = Breeding Reserves, N.P.= National Park.*

of Scania, the most southern province of Sweden. The mandibles originate from forested areas dominated by spruce (*Picea abies*) and beech (*Fagus sylvatica*). Only the date of slaughter is known. The mandibles originate from the collection of the department of Historical Osteology, Lund University.

## Method

### *Age estimation based on tooth eruption*

The absolute age is known for 53 mandibles from Bialowieza Breeding Reserves and 16 from Kampinos National Park. The ages of the other 246 mandibles have been assessed from tooth eruption. In order to study the reliability of using tooth eruption for ageing in this study, the mandibles of known age were also assessed from eruption according to Matschke (1967).

Age estimation based on tooth eruption correlates well with the known age of the mandibles (Fig. 2). A divergence of the estimated age from the known age with a few months can be seen in Fig. 2. This divergence is expected since there is a natural variation of the ages at eruption of different teeth. It has previously been shown that the ages of tooth eruption vary between different populations of wild boar and even between individuals from the same litter (Matschke 1967, 111; Boitani and Mattei 2001, 419–420; Genov *et al*. 1991, 401). The mean difference in this comparison is 1.6 months between the estimated and known age. The discrepancy between the estimated and known age seems to increase with age. In mandibles from individuals of 0–12 months, the mean difference was only 1.1 months, while in individuals of 18–24 months, it was 2.7 months. Of the 57 mandibles with known age (mandibles with erupted $M_3$ in wear were not used in this comparison), there are six in which

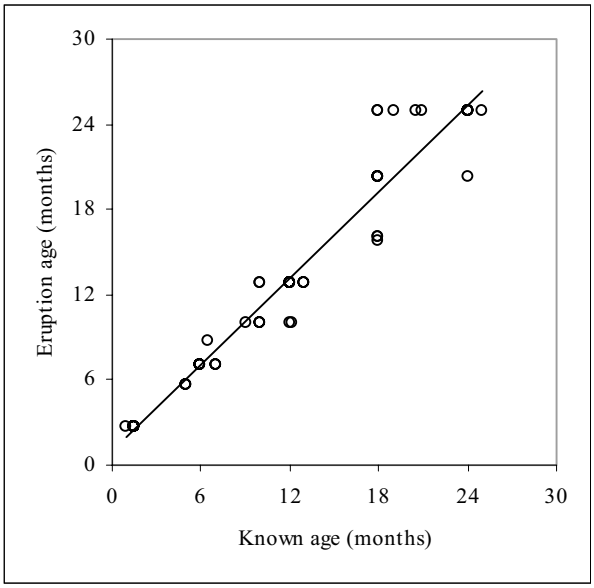


*Fig. 2. Regression line (*r= *0.971,* P= *<0.0001) and scatterplot of 57 mandibles of known age and age estimation based on tooth eruption in wild boar from Bialowieza Breeding Reserves and Kampinos National Park, Poland. The mean eruption age is according to Matschke (1967).*

the age estimated from eruption is more than three months from the known age. Five mandibles were estimated to 23–26 months, but were in fact 18–21 months.

The ages of tooth eruption in mandibles of known age from the Bialowieza Breeding Reserves and Kampinos National Park are similar to those in other studies of the tooth eruption in wild boar, except for the second and third molar (Fig. 3). In three mandibles out of 12, the

| | $M_1$ | $C_1$ | $M_2$ | $I_2$ | $M_3$ |
|---|---|---|---|---|---|
| Germany - Briedermann (1967) | 5–6 | 10–12 | 12–13 | 18–20 | 21–24 |
| USA - Matschke (1967) | 5–6 | 7–11 | 12–14 | 18–22 | 23–26 |
| Bulgaria – Genov *et al*. (1991) | 5–6 | 10–12 | 13–14 | 18–24 | 19–24 |
| Italy – Boitani and Mattei (1991) | 5 | 9–10 | 12–13 | 20–21 | 20–26 |
| Bialowieza Breeding Reserve | $5^2$ | $7–12^{11}$ | $12–13^{10}$ | $18^3$ | $18–25^9$ |
| Kampinos National Park | | $10–12^4$ | $10–12^3$ | $18–24^3$ | $18–24^3$ |

*Fig. 3. Ages at eruption of teeth in wild boar of known age from two Polish samples in comparison with earlier studies. The superscript figures indicate sample size. All eruption data from Bialowieza Breeding Reserves are from hybrids between wild boar and domestic pig, except for three of the $M_2$ (erupting at 12 months) and four of the $M_3$ (erupting at 24–25 months).*

| Age group (months) | Tooth eruption |
|---|---|
| 0–2 | $di_{13}\ dc_1\ dp_{34}$ |
| 5–6 | $di_{123}\ dc_1\ dp_{234}$, $M_1$ erupting |
| 7–8 | $di_{123}\ dc_1\ dp_{234}\ M_1$ |
| 9–11 | $di_{12}\ dp_{234}\ I_3\ C_1\ (P_1)\ M_1$ |
| 12–13 | $di_{12}\ dp_{234}\ I_3\ C_1\ (P_1)\ M_1$, $M_2$ erupting |
| 14–18 | $I_1 di_2\ I_3\ C_1\ (P_1)\ P_{234}\ M_1\ M_2$ |
| 19–24 | $I_{123}\ C_1\ (P_1)\ P_{234}\ M_1\ M_2$, $M_3$ mesial cusps are erupting |
| 25–36 | $I_{123}\ C_1\ (P_1)\ P_{234}\ M_1\ M_2$, $M_3$ distal cusps are erupting* |
| >36 | $I_{123}\ C_1\ (P_1)\ P_{234}\ M_1\ M_2$, $M_3$ |

*Fig. 4. Age groups used in the study based on different stages in the eruption of the dentition in wild boar according to Matschke (1967), with adjustment of the eruption of the third molar. *Eruption of the distal cusps of the third molar is according to Boitani and Mattei (2001).*

third molar has already started to erupt by 18–19 months of age. This is in the same age range as the eruption of the third molar in domestic pigs (Silver 1969; Habermehl 1961). Since two of these mandibles originate from hybrids between domestic pigs and wild boar from the Bialowieza Breeding Reserves, it is not surprising that the time of eruption in some individuals are similar to that of domestic pigs. Mandibles with early erupting third molars from Kampinos National Park were also observed, but this has also been noticed in other populations of wild boar (see Fig. 3). The second molar was found to be erupting at ten months of age in two mandibles from Kampinos National Park. This occurrence is exceptional because no other study of tooth eruption in wild boar has reported eruption of the second molar before 12 months of age (Fig. 3). One explanation could be that these mandibles were from individuals which were wild and domestic pig hybrids, since the second molar erupts earlier in domestic pigs than in wild boar (Bull and Payne 1982, 56). Interbreeding between wild boar and domestic pig is a common occurrence in all parts of the world where domestic pigs are kept and wild boar occurs (Genov 1999, 205).

Because of the variation of the ages of tooth eruption, age-intervals were used instead of precise ages, thus aged mandibles were divided into different age groups (Fig. 4). The age groups are based on the eruption according to Matschke (1967), but the ages of eruption of the third molar were corrected to cover the variation seen in this tooth in different populations. The ages of eruption of the third molar in the study by Matschke (1967) consider only the eruption of the first cusps and not the whole tooth. To cover the eruption of the complete dentition in wild boar, data of the ages when the distal cusps of the third molar erupt according to Boitani and Mattei (2001) were also used. Since ageing was based on eruption, it was not possible to study the tooth wear of individuals older than 36 months in any detail, except for eight individuals with known age.

The reason that dates of slaughter have not been used in calculating an approximate age based on an assumed birth date is the frequent occurrence of litter births outside the usual farrowing season. Wild boar in Germany and Sweden usually farrow during February to May, but 8–15% of the litters are not delivered during this period (Briedermann 1986, 249; Lemel 1999, 33).

### *Tooth Wear*

The permanent molars ($M_1$, $M_2$, $M_3$) and the fourth deciduous premolar ($dp_4$) from both halves of the mandible were studied. The dentition of the right side was used in comparison within or between the samples, but when a right molar was missing the counterpart on the left side was used. The attrition of the dentition was recorded depending on wear pattern and different tooth wear stages according to Grant (1982). Both tooth wear stages (TWS) of separate teeth and the mandible wear stages (MWS) of the permanent molars in the tooth row were studied. The primary reason for using Grant's method was to make the result of the study applicable to databases of tooth wear from analysed archaeozoological materials, since the method is most commonly used for recording tooth wear in mandibles of wild boar. It is also a method that enables fast and accurate recording of tooth wear scores (Grant 1982, Levitan 1982).

The asymmetry in tooth wear was analysed by calculating the difference in tooth wear stages between the right and left molars. A difference of '0' means the same TWS or MWS on both halves of the mandible, while a negative figure indicates a greater attrition on the left side, and a positive figure the opposite.

The wear stages have been treated statistically as ordinal data and the Kolmogorov-Smirnov test was used in order to test the statistical significance of the asymmetry in tooth wear and the degree of tooth wear in mandibles of males and females. The rate of tooth wear in different populations was analysed by comparing the linear regression between age and wear stages in the samples. The slope of the regression was used as a measurement of the rate of tooth wear in a similar manner as in studies of the tooth wear in humans and red deer (Klein *et al.* 1981; Richards and Miller 1991; Mays *et al.* 1995; Mays 2002).

### Asymmetry in Tooth Wear

Tooth wear in wild boar is symmetric in most individuals and the frequency of mandibles with a large variation in tooth wear between the right and left tooth rows is low (Fig. 5). Out of all studied mandibles, 68% have the same MWS (mandible wear stage) and 27% a difference of only one MWS between the right and left tooth rows. Highly asymmetric tooth wear with a difference of three respectively five MWS was observed only on two mandibles out of a total of 306 mandibles.

The degree of asymmetry in tooth wear varies between the different samples of mandibles (Fig. 5), but the differences are not statistically significant. In the three largest samples, the frequency of mandibles with symmetric tooth wear varies from 58–75%. The differences can be explained by different age structures in the samples and a larger asymmetry in tooth wear in older age groups. In the sample from Bialowieza Primeval Forest, 35% of the mandibles are from individuals older than 24 months and the asymmetry is also larger than in the sample from Bialowieza Breeding Reserves where only 15% of the mandibles are from individuals older than 24 months.

As expected, the asymmetry in tooth wear increases with age (Fig. 6). The asymmetry in tooth wear of mandibles from individuals older than 24 months is statistically significantly larger than in the younger age groups ($p$= 0,001). Although the asymmetry increases with age, the asymmetry in individuals older than 36 months is still relatively small and only two mandibles with a larger difference than two MWS were found in this age group.

The generally symmetric tooth wear in wild boar indicates that the risk for errors in the age estimation due to an abnormal wear on one of the halves of the mandibles is small, and that it is reasonable to assume that the tooth wear stage observed on fragmented mandibles or loose teeth is representative for the dentition of the individual it originated from

### Tooth wear in Male and Female Wild Boar

No clear evidence of a differentiated rate in tooth wear between males and females could be found, as previously shown for other ungulates such as domestic goat (Deniz and Payne 1982, 181–187). The mean tooth wear stages (TWS) of the $M_1$ in wild boar from Schleswig-Holstein was slightly higher in females than in males, while in the sample from Bialowieza Primeval Forest the mean in TWS was higher in males than in females (Fig. 7). The ambiguity of the result, with a higher rate of tooth wear in females in one sample and the opposite in the other, indicates that the samples are not representative for this part of the study. It seems unlikely that the feeding behaviour and attrition of males and females should be the opposite in two populations of wild boar. The differences are small and not statistically significant on a 0.05 level. A larger sample size than available in this study would be needed in order to determine if differences in the rate of tooth wear in male and female wild boar truly exist. This analysis indicates that the difference of the rate in tooth wear between males and females younger than 36 months is relatively small, if existing at all, and that it is reasonable to combine the wear stages for both males and females.

### Inter-population Variability in Tooth Wear

The linear relationship between the mandible wear stage (MWS) and age is statistically significant and the correlation coefficient indicates a strong relationship between MWS and age (see Fig. 8). The slopes of the linear regressions are similar in the five populations, showing

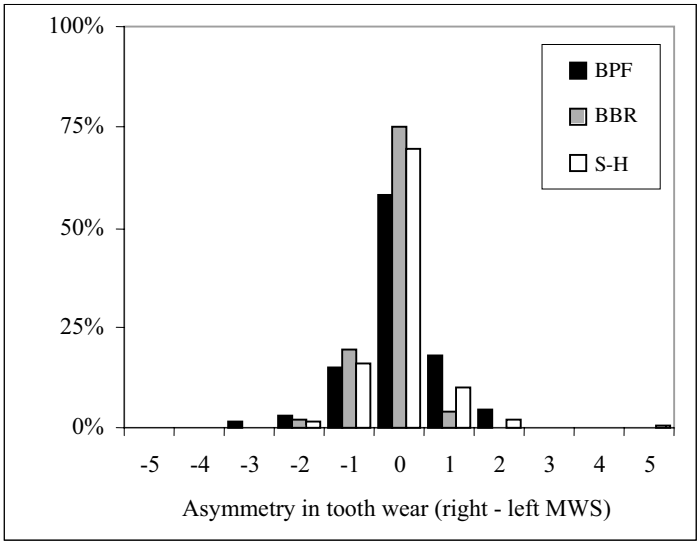


*Fig. 5. Frequency of asymmetry (difference between right and left MWS) in tooth wear in wild boar. BPF= Bialowieza Primeval Forest (n= 66), BBR= Bialowieza Breeding Reserves (n= 52), S-H= Schleswig-Holstein (n=139).*

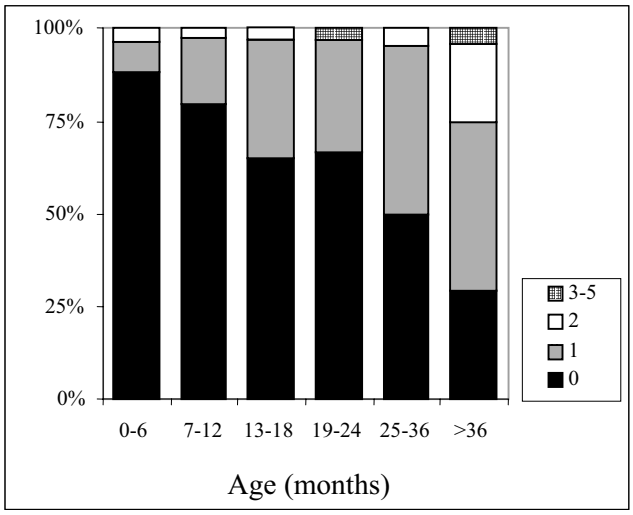


*Fig. 6. Frequency of asymmetry (difference between right and left MWS) in tooth wear in different age groups of wild boar combined from five populations.*

a relatively uniform rate of tooth wear (Figs 8, 9). The slope of the regression line for the samples from Bialowieza Breeding Reserves and Schleswig-Holstein in comparison with the other samples may indicate a higher rate of tooth wear in these populations. However, when taking into account the standard error of the slope for the regression lines, all populations lie inside the 95% confidence limits for the slopes.

Some of the differences between the populations could be the result of methodological factors. Different age structures of the samples do not make them completely comparable. The age structures of the samples and the limitations of the age estimation, especially in the older age groups where the estimated age is the mean value of an interval of 6–12 months, could be sources of error. For instance, if in one sample mandibles are estimated to be in the age group 14–18 months but they in fact are 18 months, while in another sample mandibles estimated to the same age group are 14 months, the MWS will be higher in the first sample indicating a higher rate of tooth wear. The result would then be an artefact of the age estimation and different age structures of the samples. It is probably no coincidence that the strongest correlation between wear stages and age is found in the sample with

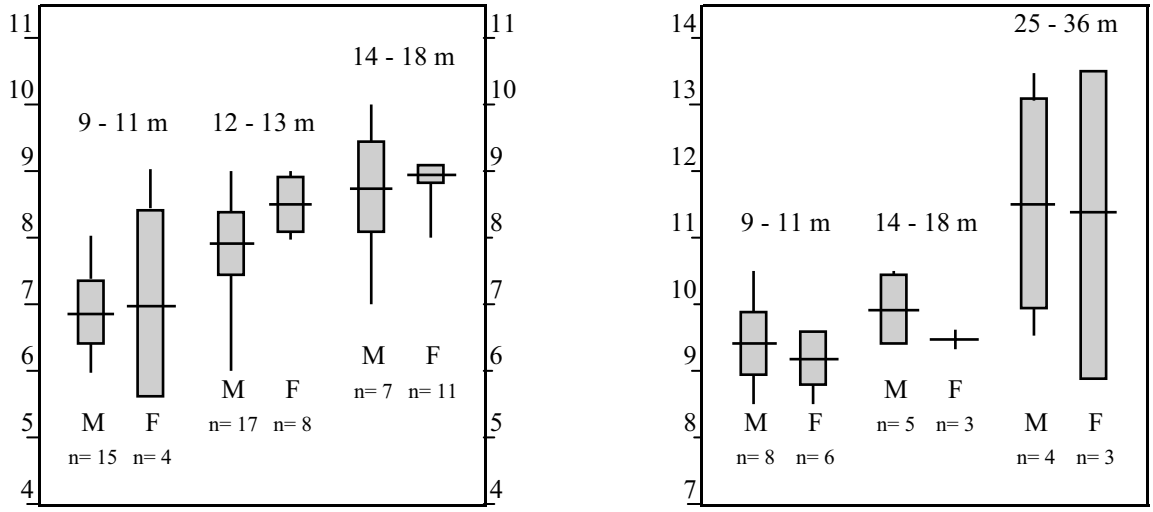


*Fig. 7. The range, mean and standard error of the mean (95% confidence limits) of TWS in the $M_1$ of male and female wild boar from Schleswig-Holstein (left) and Bialowieza Primeval Forest (right). M= males, F= females, m= months.*

| | | n | Slope | 95% CI of slope | Corr. Coeff. |
|---|---|---|---|---|---|
| MWS | BBR | 50 | 0.900 | 0.947 – 0.852 | 0.983 |
| | BPF | 52 | 0.787 | 0.856 – 0.718 | 0.954 |
| | KNP | 24 | 0.777 | 0.961 – 0.593 | 0.935 |
| | S | 22 | 0.770 | 0.897 – 0.643 | 0.871 |
| | S-H | 136 | 0.854 | 0.911 – 0.797 | 0.929 |
| dp4 | BBR | 31 | 0.646 | 0.764 – 0.528 | 0.844 |
| | BPF | 32 | 0.599 | 0.875 – 0.323 | 0.612 |
| | KNP | 16 | -0.035 | 0.363 – -0.433 | 0.047 |
| | S | 12 | 0.227 | 0.394 – 0.060 | 0.646 |
| | S-H | 98 | 0.317 | 0.419 – 0.215 | 0.526 |
| M1 | BBR | 38 | 0.326 | 0.367 – 0.285 | 0.933 |
| | BPF | 50 | 0.133 | 0.180 – 0.086 | 0.627 |
| | KNP | 24 | 0.186 | 0.296 – 0.076 | 0.577 |
| | S | 22 | 0.197 | 0.269 – 0.124 | 0.769 |
| | S-H | 136 | 0.254 | 0.289 – 0.219 | 0.768 |
| M2 | BBR | 29 | 0.252 | 0.311 – 0.193 | 0.848 |
| | BPF | 24 | 0.222 | 0.321 – 0.121 | 0.676 |
| | KNP | 11 | 0.378 | 0.621 – 0.135 | 0.711 |
| | S | 15 | 0.288 | 0.398 – 0.178 | 0.818 |
| | S-H | 77 | 0.349 | 0.400 – 0.298 | 0.840 |

*Fig. 8. Linear regression analyses of MWS and TWS of wear stages of $dp_4$, $M_1$ and $M_2$ versus age in five populations of wild boar. BBR= Bialowieza Breeding Reserves, BPF= Bialowieza Primeval Forest, KNP= Kampinos National Park, S= Scania, S-H= Schleswig-Holstein*

the mandibles of known age, Bialowieza Breeding Reserves (Fig. 8).

When the tooth wear stages (TWS) of isolated teeth are compared, it is evident that the rates of tooth wear differ between the populations. The slope of the regression between TWS of the $dp_4$ and the age for Bialowieza Breeding Reserves and Bialowieza Primeval Forest indicates a higher rate of tooth wear in these samples in comparison with the other samples. One contributing cause to the different slopes is different age structures of the samples. The two samples from Bialowieza, with a slope indicating a relatively fast rate of wear, are the only samples with individuals from the youngest age group (Fig. 1). If the youngest age group (0–2 months) is excluded, the slope of the linear regression becomes more similar to that of the other samples.

When excluding the youngest age group from the sample from Bialowieza Primeval Forest, the slope changes a lot and the regression shows a weak correlation with age (slope= 0.101, correlation coefficient= 0.104). Even if the slope also changes when the youngest age group is excluded from the sample from Bialowieza Breeding Reserves (slope= 0.429, correlation coefficient= 0.610), the slope still indicates a relatively high rate of tooth wear in this sample. In the scatterplot (Fig. 10), it can be noted that the TWS of the wild boar from Bialowieza Breeding Reserves generally is higher than in wild boar of the same age groups from Schleswig-Holstein.

The slope of the regression of TWS upon age for the $M_1$ shows that the highest rate of tooth wear is found in the population from Bialowieza Breeding Reserve followed by the sample from Schleswig-Holstein, while the lowest rate of wear is found in the population from Bialowieza Primeval Forest (Figs 8 and 11). The

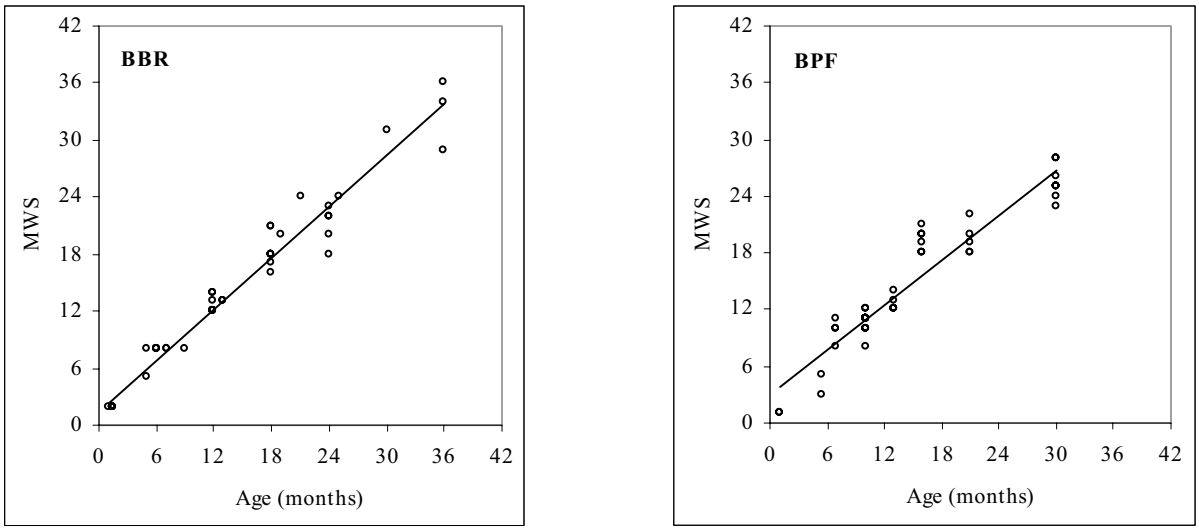


*Fig. 9. Regression line and scatterplot of MWS versus age for wild boar from Bialowieza Breeding Reserves (BBR) and Bialowieza Primeval Forest (BPF).*

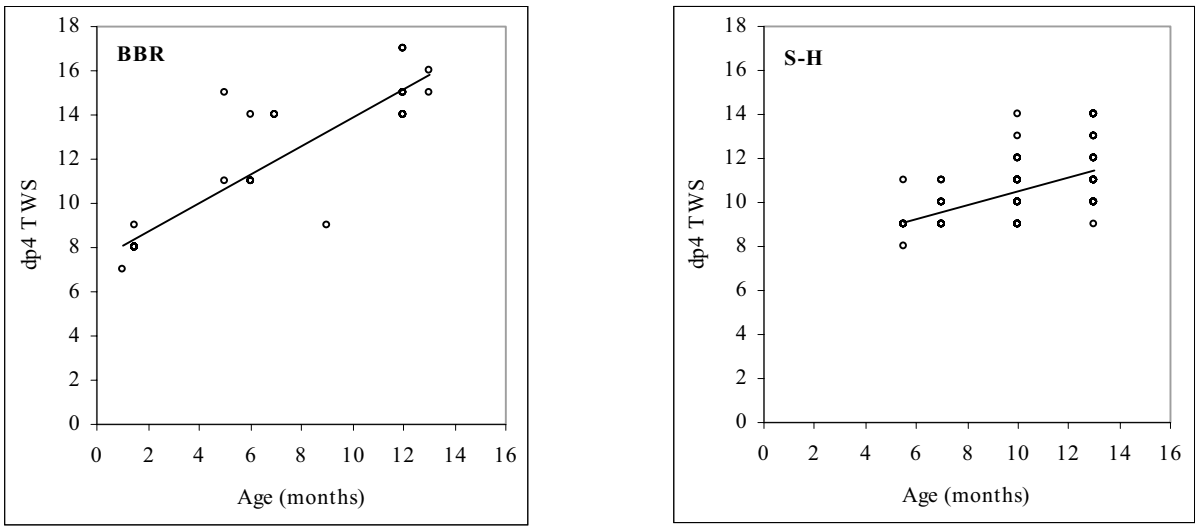


*Fig. 10. Regression line and scatterplot of TWS in $dp_4$ versus age for wild boar from Bialowieza Breeding Reserves (BBR) and Schleswig-Holstein (S-H).*

scatterplot (Fig. 11) of the TWS of the $M_1$ versus age for wild boar from Bialowieza Primeval Forest shows that the rate of wear slows down after about 12 months and the tooth then stays in wear stage 9 (d) and 10 (e) for a long period. This does not seem to be the case for wild boar from Bialowieza Breeding Reserves where the $M_1$ continues to wear at a similar rate with increasing age. The higher correlation coefficient of the regression line for $M_1$ and $M_2$ in comparison with the $dp_4$ indicates a stronger relationship between tooth wear and age in the permanent molars (Fig. 8).

The slopes of the regression lines for $M_2$ are similar in the different populations and the slopes overlap when the 95% confidence is taken account for (Figs 8 and 12). If the slopes of the permanent molars are compared, the slopes for the $M_2$ are indicating a higher rate of wear than the $M_1$ in all samples, except for the sample from Bialowieza Breeding Reserves (Fig. 8). The explanation of why the slope of the $M_2$ is indicating a higher rate of wear for this tooth is probably the result of differentiated duration of different TWS and the later eruption of the $M_2$.

Tooth wear stages 1–8 are observable during relatively short time periods. The stages cover the formation of

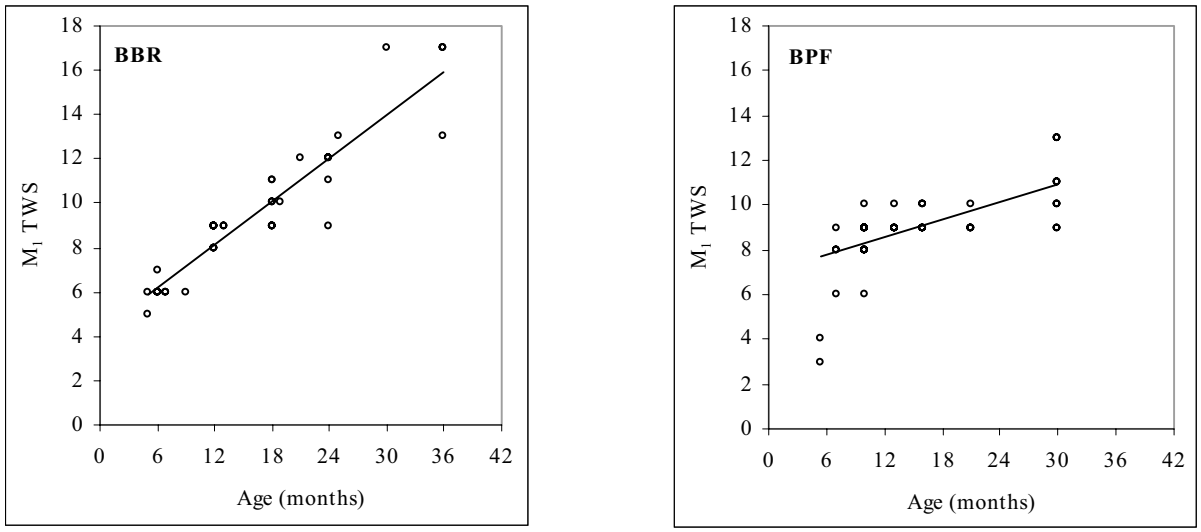


*Fig. 11. Regression line and scatterplot of TWS in $M_1$ versus age for wild boar from Bialowieza Breeding Reserves (BBR) and Bialowieza Primeval Forest (BPF).*

crypt, eruption and wear patterns with exposure of dentine on the cusps. The following stage 9 (d) is defined as the exposure of dentine on all cusps and is a long lasting wear stage. The next stage (e) is not reached until the cusps have been worn down to a level where the dentine links the paraconid and the protoconid (mesial cusps). Another factor contributing to the longevity of wear stage d (score 9) for the $M_1$, is that the wear stage generally is reached at about 12 months when the $M_2$ erupts (Fig. 11). After the eruption of the $M_2$, much of the attrition exposed to the $M_1$ before the eruption is probably reduced and transferred to the $M_2$. It is also most likely that the result of the long lasting wear stage d (9) is the cause of the plateau seen in the scatterplot of TWS versus age from Bialowieza Primeval Forest (Fig. 11).

The indications of a higher rate of wear in the population from Bialowieza Breeding Reserves (BBR), at least for the $M_1$ and $dp_4$, are probably the result of a higher proportion of abrasive particle in the diet. The wild boar from BBR have been kept in enclosures, which usually have a very sparse vegetation on the ground followed by soil exposure in the areas of feeding due to rooting and trampling. In surroundings like this, it is likely that the ingestion of soil is higher, resulting in a more rapid rate of tooth wear than for free-ranging wild boar feeding in forests and fields. Studies of the relationship between wear and ingestion of soil in domestic sheep from New Zealand have shown that the rate of tooth wear is influenced by the degree of ingestion of soil (Healy and Ludwig 1965).

The analysis of the rate of tooth wear in the different populations does not seem to give any clear or consistent results. This is probably due to heterogeneity of the age structures of the samples and the fact that the slope of the linear regression between wear stage and age is not a perfect method for measuring the rate of tooth wear. However, some tendencies indicate differences of the wear rates between the samples. The wild boar from the Bialowieza Breeding Reserves have most likely an increased rate of tooth wear in comparison with the other populations, as a result of living in a different environment in enclosures with a more frequent exposure of abrasive particles in the food as mentioned above. Further, it seems as if the rate of tooth wear is somewhat higher in wild boar from Schleswig-Holstein than in the other three populations, with the lowest degree of wear in the population from Bialowieza Primeval Forest, at least if one only considers the wear of the permanent molars (Fig. 8). Due to limited information available about factors like diet, feeding behaviour and soil conditions that may have affected the rate of tooth wear, it is only possible to speculate about the differences between the populations. Analysis of dental microwear could have been used in an effort to identify differences in the diet between the populations (Ward and Mainland 1999), but this is beyond the scope of this study.

The median and range of MWS and TWS in different age groups of the four free-ranging populations of wild boar overlap to a large extent, and indicate that the relationship between tooth wear and age is similar in these populations, at least in individuals younger than 36 months (Figs 13, 15–18). This result is in agreement with inter-population comparisons of tooth wear for other wild animals, such as fallow red and red deer, in which rates of attrition are similar in different populations (Lowe 1967, 148–149, Chaplin and White 1969; Spinage and Brown 1988; Brown and Chapman 1991, 535).

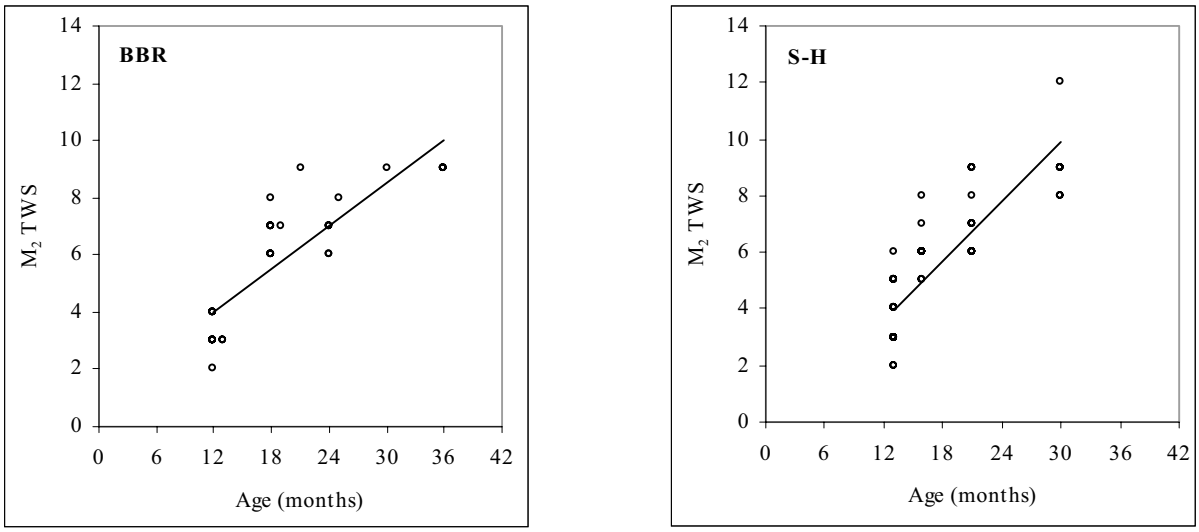


*Fig. 12. Regression line and scatterplot of TWS in $M_2$ versus age for wild boar from Bialowieza Breeding Reserves (BBR) and Schleswig-Holstein (S-H).*

**Age Estimation Based on Tooth Wear**

The results show that tooth wear correlates well with age and indicate that tooth wear evidently can be useful for age estimation of archaeozoological remains of wild boar, but also that the individual variation in tooth wear is large and must be taken into account for age estimation. Mandible wear stages (MWS) are, as expected, more appropriate to use for age estimation than tooth wear stages of isolated teeth, which is shown by the high correlation coefficient of the linear regression between MWS and age (Fig. 8).

The early wear stages are found only in limited age intervals of 2–6 months, but with increasing wear, the age range where a wear stage can be identified is also increasing (Fig. 13). This is shown in a scatterplot between MWS and age, which illustrates how the age interval increases with increasing tooth wear stages (Fig. 14). A mandible wear score (MWS) of 5 is only found in mandibles from individuals of 5–6 months, while MWS 10 and 20 are found in mandibles of 7–13 respectively 19–24 months. The age interval for MWS 30 is 42–78 months. The pattern with an increasing spread of MWS with increasing age is expected because individual differences in wear will accumulate with age and is a characteristic of the tooth wear of different mammalian species, such as red deer, domestic goat and humans (Deniz and Payne 1982, 197–204; Brown and Chapman 1991, 531; Mays 2002, 866).

Unfortunately, it was not possible to analyse the relationship between tooth wear and age in individuals above 36 months in any detail, since only eight mandibles of this age group with known age at death were available. The differences in the rate of tooth wear between the populations occurring in mandibles less than 36 months seem to increase with age and are more apparent in the older age groups (Fig. 14). In the sample from Kampinos National Park, MWS 28 is found in wild boar of 46–48 months while MWS 29–36 is found in individuals of only 30 and 36 months in the sample from Bialowieza Breeding Reserves.

The result, revealing a relatively strong relationship between tooth wear stages (TWS) and age, clearly demonstrates the possibilities of using loose teeth for age estimations (see Fig. 8). The analysis shows that, due to the large individual variation in tooth wear within populations, a detailed division of the wear of the $dp_4$ into twelve stages according to Grant (1982) does not allow for a more refined age estimation of wild boar (Fig. 15, Fig. 10). The wear stages a–c (6–8) are only found in individuals of 1–6 months, while teeth in wear score d-m (9–17) are found in wild boar of 6 months as well as 13 months (Fig. 15). There is a tendency that the higher wear stages are more common in individuals of about 12 months, but the individual variation is great, even within the same population. This problem is clearly illustrated in Fig. 10 with $dp_4$ from individuals of 6–13 months with the same TWS. The large variability in tooth wear of $dp_4$ has also been observed in other species, such as domestic sheep (Moran and O´Connor 1994, 277).

The relationship between tooth wear stage and age for the $M_1$ and the $M_2$ is comparable due to the similarities of their morphology and the fact that the same wear stages are used for both these teeth. The first wear stages of the $M_1$ and the $M_2$, a–c (6–8), last for short periods and thus these stages are useable for age estimation into short age intervals. Wear stage d (9), as mentioned above, is a long lasting stage, which results in the fact that teeth of this stage can only be estimated to relatively large age

| MWS | | BBR | BPF | KNP | S-H | S |
|---|---|---|---|---|---|---|
| | median | 1,5 | 0 – 2 | | | |
| 0–2 | range | 1 – 2 | 0 – 2 | | | |
| | n | 12 | 2 | | | |
| | median | 5 | 5 – 6 | | 5 – 6 | |
| 3–5 | range | 5 | 5 – 6 | | 5 – 6 | |
| | n | 1 | 2 | | 4 | |
| | median | 6 | 7 – 8 | 6 – 8 | 7 – 11 | 9 – 11 |
| 6–10 | range | 5 – 9 | 7 – 11 | 6 – 12 | 5 – 11 | 7 – 13 |
| | n | 8 | 7 | 10 | 40 | 7 |
| | median | 12 | 8 – 11 | 9 – 11 | 12 – 13 | 12 – 13 |
| 11–15 | range | 12 – 13 | 7 – 13 | 6 – 13 | 9 – 18 | 9 – 13 |
| | n | 10 | 22 | 6 | 52 | 5 |
| | median | 18 | 14 –18 | 21 | 14 – 18 | 14 – 18 |
| 16–20 | range | 18 – 24 | 14 – 24 | 14 – 24 | 12 – 24 | 14 – 24 |
| | n | 8 | 9 | 5 | 29 | 8 |
| | median | 21 | 25 – 36 | 18 | 25 – 36 | 25 – 36 |
| 21–25 | range | 18 – 25 | 14 – 36 | 14 – 21 | 19 – 36 | 19 – 36 |
| | n | 7 | 7 | 3 | 5 | 2 |
| | median | 39,5 | >36 | 48 | 25–36 | |
| 26–30 | range | 36 – 42 | 25 – >36 | 46 – 84 | 25 – >36 | |
| | n | 2 | 7 | 4 | 8 | |
| | median | 33,5 | >36 | 60 | >36 | |
| 31–35 | range | 30 – 36 | >36 | 60 | 25 – >36 | |
| | n | 2 | 7 | 1 | 2 | |
| | median | 42 | >36 | | >36 | |
| 36–40 | range | 36 – 60 | >36 | | >36 | |
| | n | 3 | 4 | | 1 | |
| | median | | >36 | | >36 | |
| 41–50 | range | | >36 | | >36 | |
| | n | | 1 | | 1 | |

*Fig. 13. The age distribution of mandible wear stages (MWS) in five populations of wild boar.*

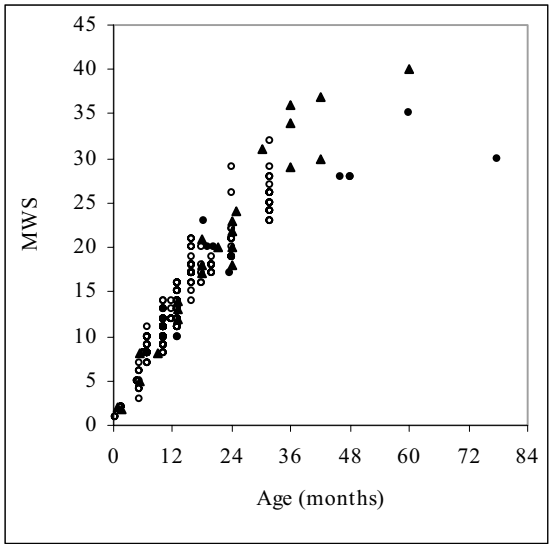


*Fig. 14. Scatterplot of MWS and age in five populations of wild boar. Triangles= Bialowieza Breeding Reserves (known age), black dots= Kampinos National Park (known age), circles= Bialowieza Primeval Forest, Schleswig-Holstein and Scania (estimated age).*

intervals (Figs 11–12 and Figs 16–17). For the higher TWS, it was only possible to conclude that $M_1$ and $M_2$ in wear stage h (13) from e (10) most likely derive from individuals older than 36 months (Figs 16–17). This is due to limitations of the material used in this study.

The wear of $M_3$ was not analysed to the same extent as that of the other two molars due to the fact that the main part of the material consisted of juvenile individuals with unerupted $M_3$. Based on this study, only the first two wear stages, a–b (6–7), can be used for age estimation of teeth into specific intervals, while $M_3$ with wear stage c (8) and above are most likely to be found in individuals older than 36 months (Fig. 18). Tooth wear stages 9–15 (d–k) of the third molar was not observed on any mandibles of animals of known age between 36–60 months. This indicates that specimens with third molars in these wear stages probably represent older wild boar at least five years of age or more.

The analysis of inter-population variability in tooth wear indicates that the rate of attrition varies between different populations of wild boar. The results show that the population from the Bialowieza Breeding Reserves, with wild boar kept in enclosures, have a higher rate of tooth wear from the other four populations of free-ranging wild boar. The relationship between tooth wear and age of wild boar from the four free-ranging populations is relatively similar and indicate a uniformity in tooth wear, at least in individuals less than 36 months between wild boar from temperate forests in Northern Europe.

The most striking variability of tooth wear is not the differences between populations, but rather the individual variation within populations. The large individual variation of tooth wear within populations can be seen in the scatterplots of wear stages versus age (Figs 9, 10, 11, 12, 14) and is one of the reasons for the relatively large age intervals in which certain TWS occur (Figs 13, 15, 16, 17, 18).

When age estimation is based on attrition, the appropriate age intervals for wear stages must be used while taking into account the large individual variation in tooth wear found in wild boar. Assumptions made, that the rates of tooth wear are similar among wild boar and domestic pigs represented in a given assemblage (Rolett and Chiu 1994, 378), for example, can be questioned based on the results of this study. Ageing based on tooth wear of wild boar and domestic pigs into relatively narrow age intervals of a couple of months should be reassessed – broader age groups are more appropriate (Rowley-Conwy 1993; Rowley-Conwy and Storå 1997; Horard-Herbin 1997).

| TWS | | BBR | BPF | KNP | S-H | S |
|---|---|---|---|---|---|---|
| | median | 1 | | | | |
| a-b | range | 1 | | | | |
| | n | 1 | | | | |
| | median | 1,5 | | | 5 – 6 | |
| c | range | 1,5 | | | 5 –6 | |
| | n | 10 | | | 1 | |
| | median | 6 | 9 – 11 | | 9 – 11 | 7 – 8 |
| d | range | 1,5 – 9 | 5 – 11 | | 7 – 13 | 7 – 8 |
| | n | 2 | 6 | | 24 | 2 |
| | median | | 9 – 11 | | 9 – 11 | 12 – 13 |
| e | range | | 9 – 13 | | 7 – 13 | 12 – 13 |
| | n | | 3 | | 20 | 1 |
| | median | 6 | 9 – 11 | 9 – 11 | 9 – 11 | 9 – 11 |
| f | range | 5 – 6 | 9 – 11 | 9 – 13 | 5 – 13 | 9 – 13 |
| | n | 4 | 7 | 2 | 34 | 9 |
| | median | 12 | 9 – 11 | 9 – 11 | 12 – 13 | |
| g-m | range | 5 – 13 | 7 – 13 | 7 – 13 | 9 – 13 | |
| | n | 14 | 14 | 14 | 19 | |

*Fig. 15. The age distribution of tooth wear stages (TWS) of $dp_4$ in five populations of wild boar.*

| TWS | | BBR | BPF | KNP | S-H | S |
|---|---|---|---|---|---|---|
| | median | 6 | 9 – 11 | 6 – 8 | 9 – 11 | 9 – 11 |
| a | range | 5 – 9 | 7 – 11 | 6 –12 | 7 – 13 | 7 – 13 |
| | n | 7 | 2 | 3 | 27 | 6 |
| | median | 6 | | 7 – 8 | 9 – 11 | 12 – 13 |
| b | range | 6 | | 7 – 8 | 7 – 18 | 9 – 13 |
| | n | 1 | | 1 | 20 | 5 |
| | median | 12 | 9 – 11 | 9 – 11 | 12 – 13 | 12 – 13 |
| c | range | 12 | 7 – 11 | 7 – 13 | 7 – 18 | 9 – 18 |
| | n | 3 | 6 | 7 | 29 | 2 |
| | median | 13 | 9 – 11 | 14 – 18 | 14 – 18 | 19 – 24 |
| d | range | 12 – 24 | 7 – 36 | 9 – 24 | 9 – 36 | 14 – 36 |
| | n | 11 | 29 | 8 | 44 | 7 |
| | median | 18 | 19 – 24 | 18 | 19 – 24 | 19 – 24 |
| e | range | 18 – 19 | 9 – >36 | 14 – 18 | 19 – 24 | 19 – 24 |
| | n | 3 | 9 | 2 | 3 | 2 |
| | median | 18 | 25 – 36 | | 25 – 36 | |
| f | range | 18 – 24 | 25 – 36 | | 25 – 36 | |
| | n | 3 | 2 | | 1 | |
| | median | 24 | >36 | 46 | 25 – 36 | |
| g | range | 21 – 24 | >36 | 18 – 78 | 25 – 36 | |
| | n | 4 | 1 | 3 | 2 | |
| | median | 36 | >36 | 48 | >36 | |
| h | range | 25 – 42 | >36 | 14 – 48 | 18 – >36 | |
| | n | 3 | 4 | 3 | 4 | |
| | median | | >36 | | 19 – 24 | |
| j-l | range | | >36 | | 19 – 24 | |
| | n | | 8 | | 1 | |
| | median | 36 | >36 | 60 | >36 | |
| m | range | 30 – 42 | >36 | 60 | >36 | |
| | n | 4 | 2 | 1 | 2 | |
| | median | 60 | | | | |
| n | range | 60 | | | | |
| | n | 1 | | | | |

*Fig. 16. The age distribution of tooth wear stages (TWS) of $M_1$ in five populations of wild boar.*

The large variation of tooth wear found within populations depends on several factors, but two of the most important ones are most likely variability in eruption and diet. The age of eruption differs between individuals from the same population. Individuals with early erupting teeth will sooner come into wear than individuals with later erupting dentition. The variability of ages of eruption is relatively small (2 months) in the $M_1$, while in the $M_3$ it may differ six months between early and late erupting individuals (Fig. 3).

The diet and feeding behaviour in wild boar varies depending on season and also from year to year, which may result in differential attrition between individuals born during different seasons and years. In Germany, the consumption of food items from rooting is relatively high during late winter and early spring. During late spring and early summer the frequency of plants in the diet increases, and during autumn and early winter, acorn and beechnut make an important food source (Briedermann 1986, 175–203). It is likely that the frequency of abrasive particles in the food also varies due to the seasonal composition of diet. Intensive rooting, for example, probably increases soil ingestion, which results in an increasing rate of tooth wear.

Due to the fact that wild boar farrow during different parts of the year, the rate of tooth wear will probably differ between individuals born during the winter, which are forced to start feeding on more abrasive food items from the ground, and those that are born in the spring that start to feed on soft plants. During years of large crops of acorn and beechnut, the diet is based on these food items and the frequency of food from rooting in the ground is much lower (Briedermann 1986, 184). This means that wild boar born during different years have various diets and exposure to abrasive particles in the food. This may affect the rate of attrition differently and result in individual variations in tooth wear within populations.

An effort here has been made to present data in a way that make tooth wear applicable for age estimation of mandibles as well as loose teeth. The different samples have been kept separate in order to facilitate age estimation based on the sample, perhaps more useful as a reference when ageing archaeozoological remains of different date and geographic origin.

A problem with age estimation is that the age

| TWS | | BBR | BPF | KNP | S-H | S |
|---|---|---|---|---|---|---|
| | median | 18 | 14 – 18 | 14 – 18 | 14 – 18 | 14 – 18 |
| a | range | 18 – 24 | 14 – 18 | 14 – 24 | 12 – 24 | 14 – 24 |
| | n | 5 | 1 | 3 | 20 | 7 |
| | median | 19 | 19 – 24 | 18 – 24 | 19 – 24 | 14 – 18 |
| b | range | 18 – 24 | 14 – 24 | 18 – 24 | 14 – 24 | 14 – 18 |
| | n | 7 | 4 | 2 | 5 | 1 |
| | median | 22 | 25 – 36 | 21 | 25 – 36 | 19 – 24 |
| c | range | 18 – 25 | 14 – 36 | 21 | 14 – 36 | 19 – 24 |
| | n | 2 | 3 | 1 | 4 | 1 |
| | median | 36 | 25 – 36 | 46 | 25 – 36 | 25 – 36 |
| d | range | 21 – 42 | 14 – >36 | 18 – 48 | 19 – >36 | 25 – 36 |
| | n | 6 | | 5 | 11 | 1 |
| | median | | >36 | 72,5 | >36 | |
| e | range | | >36 | 60 – 84 | >36 | |
| | n | | 4 | 2 | 1 | |
| | median | 51,5 | >36 | | >36 | |
| f-m | range | 42 – 60 | >36 | | 24 – >36 | |
| | n | 2 | 8 | | 3 | |

*Fig. 17. The age distribution of tooth wear stages (TWS) of $M_2$ in five populations of wild boar.*

| TWS | | BBR | BPF | KNP | S-H | S |
|---|---|---|---|---|---|---|
| | median | | 25 – 36 | 48 | 25 – 36 | 25 – 36 |
| a | range | | 25 – >36 | 46 – 48 | 25 – 36 | 25 – 36 |
| | n | | 9 | 3 | 3 | 1 |
| | median | 36 | >36 | | 25 – 36 | |
| b | range | 36 | >36 | | 25 – 36 | |
| | n | 1 | 2 | | 3 | |
| | median | 42 | >36 | 72,5 | >36 | |
| c | range | 36 – 60 | >36 | 60 – 84 | 25 – >36 | |
| | n | 5 | 4 | 2 | 5 | |
| | median | | >36 | | >36 | |
| d-j | range | | >36 | | >36 | |
| | n | | 9 | | 3 | |

*Fig. 18. The age distribution of tooth wear stages (TWS) of $M_3$ in five populations of wild boar.*

structures of the reference samples influence the assessment of age in the target sample. For example, age estimation of archaeozoological material with a method of ageing based on a reference sample consisting of mainly juveniles will result in a kill-off pattern that will be biased towards young individuals. The problem of bias in age estimation, i.e. that the age structure of the target sample mimic the structure of reference samples, was first shown by Bocquet-Appel and Masset (1982) and has since then been thoroughly discussed among physical anthropologists and paleodemographers (Jackes 1992; Konigsberg and Frankenberg 1992; 1994; Hoppa and Vaupel 2002). By using Bayesian statistical methods, it is possible to reduce bias, i.e. the undue influence of the age structure of reference samples on age estimations (Konigsberg and Frankenberg 1994; Chamberlain 2000; Millard in this volume).

## Conclusions

Large asymmetry in tooth wear seems to be rare in wild boar, which means that it is reasonable to assume that tooth wear stages of fragmented mandibles or loose teeth are representative of the dental series they originate from. No significant differences in tooth wear between males and females younger than 36 months could be found and this result implies that it is no need to treat tooth wear of males and females separately.

Analysis of inter-population variability in tooth wear indicates that the rate of attrition differs between populations of wild boar. The largest difference is between wild boar kept in enclosures and free-ranging wild boar. The rate of tooth wear in free-ranging wild boar from four populations in Northern Europe seems to be relatively similar in individuals less than 36 months old. This finding indicates that it is reasonable to apply the relationship between tooth wear stages and age from modern populations to age estimations of archaeozoological materials.

Mandible wear stages (MWS) and tooth wear stages (TWS) show a strong correlation with age, but the relatively large individual variation in tooth wear must be taken into account when using tooth wear for age estimation. The individual variations in tooth wear increase with age and this implies that early TWS are useful for age estimation into short age intervals, while later TWS with reliability can be used only to age into wide intervals. The age ranges in which wear stages can be asserted to increase with age and relatively broad age groups must be used for certain wear stages.

In order to better explain the variations noticed between, as well as within, populations of wild boar, further analysis of the influence of soil ingestion and different compositions of diet on the rate of tooth wear would be needed. Including larger reference collections of mandibles of known age into this study would refine the age estimation based on tooth wear, and limit the broad age ranges presented in this study. Further tooth wear data of individuals older than 36 months with known age would be required to assess the age of mandibles and teeth of adult wild boar into age groups.

*Acknowledgements*
I would like to thank all the people who have made it possible for me to complete this study. Elwira Szuma and her helpful colleagues deserve thanks for making the

collections of the Mammal Research Institute in Bialowieza accessible to me. I am also grateful for the hospitality and helpfulness of Dirk Heinrich and Ulrich Schmölcke during my visit and study of the collection of the Institut für Haustierkunde in Kiel. Thanks to the Swedish Institute for economic support and Per-Ola Andersson of the wild game butchery in Sjunkaröd for providing me with heads of wild boar to build up a cranium collection. Richard Carter helped me study mandibles during our mutual visit to Bialowieza. I would also like to thank Natalia Bourova, Tarek Oueslati and Kyomi Yamazaki for making literature accessible and Zydrune Palubeckaite for translation of Russian literature. I am grateful for the comments by Caroline Grigson and Haskel Greenfield on an early draft of the paper and the advices from Elisabeth Iregren and Torbjörn Ahlström. I would like to thank Camilla Magnell for proof reading. I am grateful for the travel grant awarded to me from the Institute for Aegean Prehistory which allowed me to attend the ICAZ meetings.

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*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 204–215*

# 13. Phenotype and Age in Protohistoric Horses: a Comparison Between Avar and Early Hungarian Crania

*László Bartosiewicz*

*Graves from the 6th–8th century AD Avar Empire in the Carpathian Basin often contain entire horse skeletons, while 9th–10th century AD Early Hungarian burials tend to yield skulls and bones from the feet, interpreted as remains of skinned horses.*

*The research hypothesis, that morphometric differences existed between the skulls associated with these two historical periods was tested using 12 measurements and dental age on 56 Avar and 57 Early Hungarian specimens. Avar horse skulls were better preserved while mares, in general, were underrepresented in burials.*

*Early Hungarian horses were, on average, two years younger than their Avar counterparts. Meanwhile the shorter skulls from Hungarian graves had significantly longer premolar rows. Since toothwear is known to result in the reduction of the oro-aboral length of $P^3$ to $M^2$ teeth, the only significantly different cranial proportion between the two chronological sub-samples seems to be age related, the differences in the studied skull measurements cannot be considered phenotypic.*

*When the age and sex of animals are taken into consideration, many of the differences in shape may be attributed to the divergent compositions of the two chronological sub-samples. There is a strong cultural bias in what used to look like phenotypic differences between the two studied groups of horses.*

## Introduction

A special feature of many cultures is the ritual treatment of the horse which often buried the animals' skull intact. Early osteological evidence from the Pontic-Caspian Region (4000–2500 BC), painstakingly summarized by Mallory (1981, 205–211), clearly shows the heterogeneous character and wide distribution of ritual horse bone deposits. At the other end of the time scale are medieval (Bartosiewicz 1995, 56, Fig. 35) as well as contemporary ethnographic examples of apotropaic horse skulls (Bökönyi 1978) which seem to be displayed throughout Eurasia.

In Hungary and adjacent parts of Central Europe there are two periods of particular interest, the Avar Period and that of the Hungarian Conquest. Both Avars and conquering Hungarians were pastoral peoples who migrated into the Carpathian Basin from the steppes of Central Asia. Graves of both groups provide evidence of horse sacrifice and thus, a uniquely great number of relatively well-preserved equid skulls.

Avar Period graves, largely dated to the 7–8th century AD, frequently contain complete horse skeletons. Bones of the head and dry limbs, usually interpreted as appendices to horse hides, were placed in numerous Early Hungarian, 9–10th century AD Conquest Period graves. Although ritual horse deposits are also known from earlier (Scythian, Sarmatian, Germanic etc.) contexts associated with various migrations of eastern tribes, the small numbers of those bone finds are better suited for descriptive or qualitative analyses (e.g. Bökönyi 1952; Bartosiewicz 1996; Vörös 1999a; Bartosiewicz and Bartosiewicz 2002).

The first equestrian burial ever found in Hungary dates to the aforementioned Conquest Period. It was discovered

| Measurement | Abbreviation | von den Driesch (1976) | Preservation (% of sub-sample) | |
|---|---|---|---|---|
| | | | Avar (n=56) | Hungarian (n=57) |
| Total length | A-P | Fig. 5a: 1 | 53.6 | 90.6 |
| Basal length | B-P | Fig. 5c: 3 | 69.6 | 96.2 |
| Greatest neurocranium breadth | Eu-Eu | Fig. 5a: 38 | 39.3 | 73.6 |
| Greatest breadth of skull | Ect-Ect | Fig. 5a: 41 | 85.7 | 98.1 |
| Least breadth between the orbits | Ent-Ent | Fig. 5a: 42 | 44.6 | 71.7 |
| Basion - Staphylion | B-St | Fig. 5c: 17 | 58.9 | 73.6 |
| Median palatal length | St-P | Fig. 5c: 18 | 73.2 | 84.9 |
| Length of the diastema | Ic-Pm | Fig. 5b: 21 | 66.1 | 83.0 |
| Greatest breadth of "snout" | I-I | Fig. 5a: 45 | 69.6 | 73.6 |
| Height of the foramen magnum | B-O | Fig. 5d: 37 | 53.6 | 86.8 |
| Length of the upper premolar row | $P^{2-4}$ | Fig. 5c: 24 | 80.4 | 86.8 |
| Length of the upper molar row | $M^{1-3}$ | Fig. 5c: 23 | 78.6 | 73.6 |
| Estimated dental age, years | | | 7.86 | 5.91 |

*Fig. 1. The definition and availability of cranial measurements.*

by herdsmen at Benepuszta near the city of Kecskemét in 1834 (Fodor 1998, 11). Several classic archaeozoological studies in Hungary were concerned with the evaluation of horse remains (Kubinyi 1859; Brummel 1900; Besskó 1906).

In this study, two relatively large sets of craniometric data were compared in an effort to test hypothetical differences between the skull formation of Avar and Early Hungarian horses. As an inevitable aspect of this comparison, the effects of age and sex on cranial proportions had to be considered as possible background variables behind the morphometric differences between these two groups of horse skulls.

## Material and Methods

Craniometric data on 56 Avar and 57 Early Hungarian horses in this study have been summarized from a wide range of sources. Skull measurements published by József Besskó (1906, 152–157) and Béla Hankó (1935, 66) formed the earliest portion of the data base analyzed here. Numerous data published by Sándor Bökönyi (1958, 91; 1964, 100; 1974, 530; Bökönyi and Matolcsi 1994, 356), János Matolcsi (1968, 87; 1973a, 95; 1976, 214), László Sótonyi (1962, 46) and István Vörös (1996, 191; 1997, 199; 1999b, 305) have also been included in this study, as well as cranial measurements collected in cooperation with the late István Takács (1996, 406; Takács and Bartosiewicz 1995, 600).

A major body of information taken from the seminal works of Cyril Ambros and Hans-Hermann Müller (Ambros and Müller 1980, 115–117; Müller 1985, 59; Müller and Ambros 1994, 133–136) represent areas located north of present day Hungary.

Standardized cranial dimensions (von den Driesch 1976) selected for study are listed in Fig. 1. The measurements analyzed here were those recorded most frequently throughout the 20th century and are thus most consistently available in the literature. "Preservation" in Fig. 1 means the relative frequency of measurements available in the Avar and Early Hungarian sub-samples. In spite of the almost identical assemblage sizes, Early Hungarian horse skulls were, on average, somewhat better represented (Avar 65.4%; Hungarian 80.1%). Given the heterogeneity of sources (often unrecorded conditions of deposition and the changes in recovery methods over the last century), no systemic explanation lying behind this difference could be pinpointed. Nevertheless, the resulting differential "preservation" has a bearing on the interpretation of results in this paper.

The identification of age and sex dependent skull proportions was considered of key importance in trying to establish differences between the craniometric characteristics of Avar and Early Hungarian horses. The sex and age of horses buried have not been consistently specified in earlier publications.

Data on sexual dimorphism are especially sparse in the archaeozoological literature. This aspect of cranial morphometry, therefore, was tested on a small group of skulls from adult Przewalski horses of documented sex. Measurements were taken by the late János Matolcsi on eight animals in the Zoological Institute of the [former] Soviet Academy of Sciences (previously Leningrad) and two horses in the Ukrainian Research Institute of Steppe Animal Husbandry in Askania Nova (Matolcsi 1969, 22, 36). This is not to suggest that Migration Period horses in Hungary are more closely related to modern Asiatic wild horses than other domestic breeds. Phenotypic variability, however, would have interfered less with the

| Measurement | Stallion n=5 | | Mare n=5 | | df=8 | | Pooled n=10 | |
|---|---|---|---|---|---|---|---|---|
| | mean value | standard deviation | mean value | standard deviation | t-value | p-value | mean value | standard deviation |
| A-P | 546.9 | 9.6 | 536.0 | 11.1 | 1.658 | 0.136 | 541.4 | 11.3 |
| B-P | 494.7 | 11.9 | 487.5 | 10.6 | 1.019 | 0.338 | 491.1 | 11.3 |
| B-O | 37.2 | 3.3 | 36.4 | 1.5 | 0.469 | 0.651 | 36.8 | 2.4 |
| Eu-Eu | 112.8 | 5.3 | 111.0 | 2.5 | 0.698 | 0.505 | 111.9 | 4.0 |
| Ect-Ect | 204.2 | 3.5 | 207.2 | 3.0 | -1.513 | 0.169 | 205.7 | 3.4 |
| Ent-Ent | 142.6 | 8.0 | 144.9 | 3.3 | -0.605 | 0.562 | 143.7 | 5.9 |
| B-St | 221.4 | 5.0 | 223.0 | 6.6 | -0.442 | 0.670 | 222.2 | 5.6 |
| St-P | 275.2 | 9.2 | 265.1 | 9.8 | 1.683 | 0.131 | 270.2 | 10.4 |
| Ic-Pm | 89.7 | 7.6 | 87.6 | 6.7 | 0.465 | 0.654 | 88.7 | 6.8 |
| I-I | 71.9 | 1.3 | 71.4 | 3.1 | 0.377 | 0.716 | 71.7 | 2.2 |
| $P^{2-4}$ | 98.8 | 4.7 | 98.0 | 2.5 | 0.318 | 0.759 | 98.4 | 3.6 |
| $M^{1-3}$ | 83.9 | 3.7 | 84.3 | 3.5 | -0.185 | 0.858 | 84.1 | 3.4 |

*Fig. 2. Sexual dimorphism in the cranial dimensions (mm) of Przewalski horse.*

craniometric manifestation of sexual dimorphism in wild horses.

Dental ages have been reported for at least half of the archaeological specimens under discussion here. In spite of the cumulative bias inherent to aging based on incisor teeth (Bartosiewicz 1989), correlations between these ages and certain cranial dimensions were deemed sufficient for identifying skull proportions most influenced by age. Phenotypic differences between Avar and Early Hungarian horse skulls were established using standard statistical procedures as referred to in the text.

## Results

### *Sexual dimorphism*

Data on the sex of horses from the two periods under discussion here have not been published consistently. However, the hypothesis that sexual dimorphism should be of lesser significance in the case of horses from this period has never been put forward explicitly. A Student's t-test performed on Matolcsi's raw data on Przewalski horse shows no significant difference between stallions and mares in terms of absolute measurements (Fig. 2).

While only relatively few individuals were available for this test, a stronger expression of sexual dimorphism would have been expected in wild horses as a result of reproductive competition. In domestic horse, selective breeding and possibly castration interferes with this process, buffering the manifestation of secondary sex characters.

In the archaeological series available for study, a cultural factor may further obliterate even existing differences. In a previous study by Bökönyi (1974, 268), mares were found in only 0–2.6% of Avar (n=107) and Hungarian Conquest Period (n=74) burials. Although the dominance of geldings and stallions in warriors' graves appears less overwhelming in recently investigated Avar cemeteries and mares attain somewhat higher percentages (e. g. 15%, n=96 – Ambros and Müller 1980, 22, Tab. 6; 17.2±4.9%, n=58 – Takács and Bartosiewicz 1995, 94, Tab. 2), one may presume that there is a smaller probability that Avar and Early Hungarian cranial data published without reference to sex originate from mares.

### *Comparisons between Avar and Early Hungarian horses*

In light of the aforementioned results, occasional references to sex in the literature were not *a priori* taken into consideration. Pooled cranial samples showed statistically significant differences by archaeological period only in the case of four measurements (Fig. 3).

Although ageable Early Hungarian horse skulls represented animals, on average, two years younger than their Avar counterparts, no statistically significant age difference exists between the two samples (Fig. 4). Much of the significant difference in basal length (B–P) seems to be expressed in the palatal length (St–P) as well as in the aboral, neurocranium section of the skull (B–St). One of the common morphological features in many Avar horse skulls seems to be that a longer aboral section of the parietal bones join into a sagittal crest before reaching the *squama occipitalis*. This crest looks shorter in many Early Hungarian horses or may be entirely missing (c.f. Figs 5 and 6, middle). Most conspicuously, however, shorter skulls from the Period of the Hungarian Conquest, had significantly longer premolar rows ($P^{2-4}$).

In addition to absolute measurements, cranial dimensions expressed as the percentage of basal length

| Measurement | Avar | | | Hungarian | | | t-value | d.f. | p-value |
|---|---|---|---|---|---|---|---|---|---|
| | n | mean value | standard deviation | n | mean value | standard deviation | | | |
| **Age (years)** | 43 | 7.9 | 4.2 | 26 | 5.9 | 3.7 | 1.917 | 67 | 0.060 |
| A-P | 30 | 527.4 | 19.0 | 48 | 523.3 | 20.3 | 0.888 | 76 | 0.377 |
| **B-P** | **39** | **482.0** | **17.3** | **51** | **471.1** | **18.3** | **2.884** | **88** | **0.005** |
| B-O | 30 | 37.6 | 2.6 | 46 | 37.5 | 3.2 | 0.164 | 74 | 0.870 |
| Eu-Eu | 22 | 109.5 | 5.2 | 39 | 109.5 | 5.3 | 0.037 | 59 | 0.971 |
| Ect-Ect | 48 | 207.2 | 13.1 | 52 | 205.0 | 10.1 | 0.930 | 98 | 0.355 |
| Ent-Ent | 25 | 146.1 | 10.3 | 38 | 143.2 | 11.1 | 1.023 | 61 | 0.310 |
| **B-St** | **33** | **224.8** | **10.4** | **39** | **218.7** | **7.5** | **2.903** | **70** | **0.005** |
| **St-P** | **41** | **258.5** | **13.0** | **45** | **252.3** | **12.0** | **2.299** | **84** | **0.024** |
| Ic-Pm | 37 | 95.5 | 8.4 | 44 | 93.7 | 9.5 | 0.912 | 79 | 0.365 |
| I-I | 39 | 68.2 | 4.5 | 39 | 68.2 | 6.0 | 0.036 | 76 | 0.971 |
| **$P^{2-4}$** | **45** | **88.4** | **4.4** | **46** | **91.6** | **6.0** | **-2.885** | **89** | **0.005** |
| $M^{1-3}$ | 44 | 77.7 | 3.8 | 39 | 77.0 | 5.2 | 0.713 | 81 | 0.478 |

*Fig. 3. Differences between the cranial dimensions (mm) of Avar and Hungarian horses.*

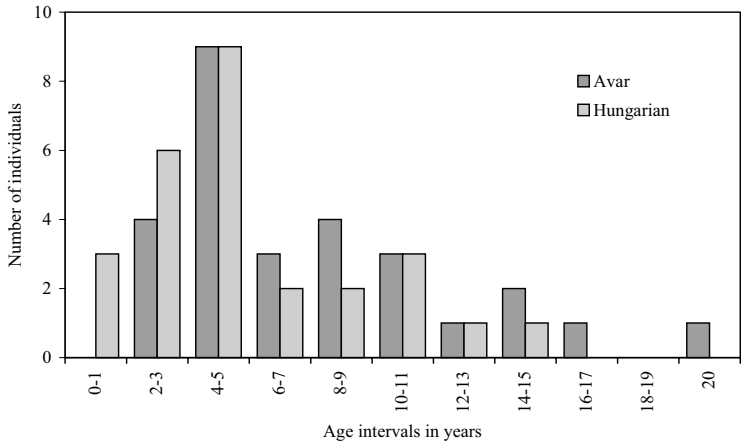


*Fig. 4. The age distribution of individuals.*

(B–P%) were also compared between the two periods. Parametric analyses of ratio values may be distorted by the skewed dispersions of their components (Atchley *et al.* 1976). Therefore, a Mann-Whitney U test was used to test differences between the cranial proportions in percentage of the basal length of the two chronological sub-samples (Fig. 7).

The only significant differences in cranial proportions between the two chronological sub-samples occurred in the case of [relative] total length and the [relative] length of the premolar row. The fact that total length (A–P) is longer relative to basal length (B–P) in Early Hungarian horses may be explained by the greater contribution of a large neurocranium to this overall measurement, a well known cranial feature of younger individuals (relative breadths in Fig. 7 are all consistently, if not significantly, higher in Early Hungarian horse skulls). The difference in measurements of the cheek tooth row should be considered all the more important since Lundholm (1947) found that toothwear results in the reduction of the oro-aboral length of $P^3$ to $M^2$ teeth while no gaps develop between these teeth. Although $M^3$ length somewhat increases with age, this seems to compensate only for the reduction of the length of the upper molar row.

Since at least one of the significantly different cranial proportions seems evidently age related, the relationship of age to other proportions was further scrutinized.

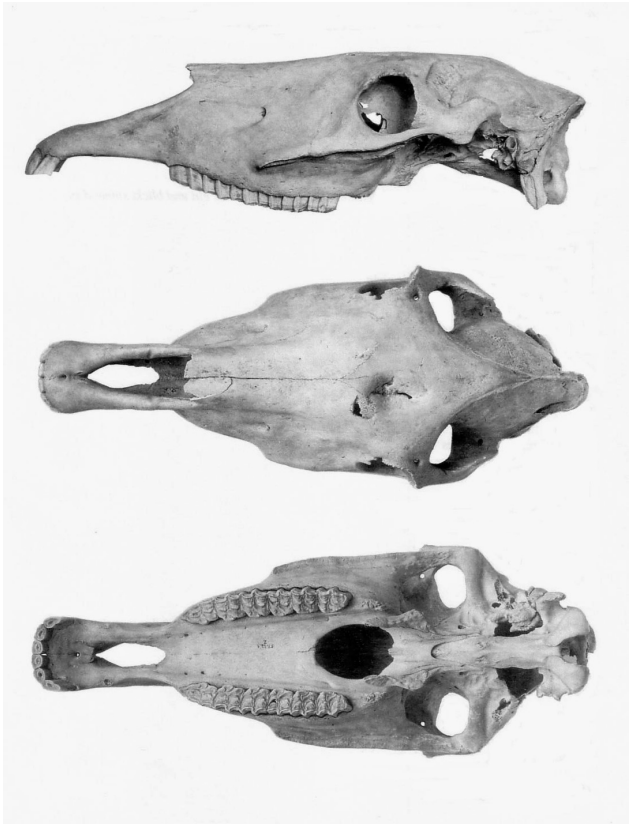

*Fig. 5. Left lateral (top), frontal (middle) and basal (bottom) aspects of an Avar Period horse skull from Pókaszepetk, Hungary. Greatest length=518 mm (Bökönyi 1974: 281, Fig. 116).*

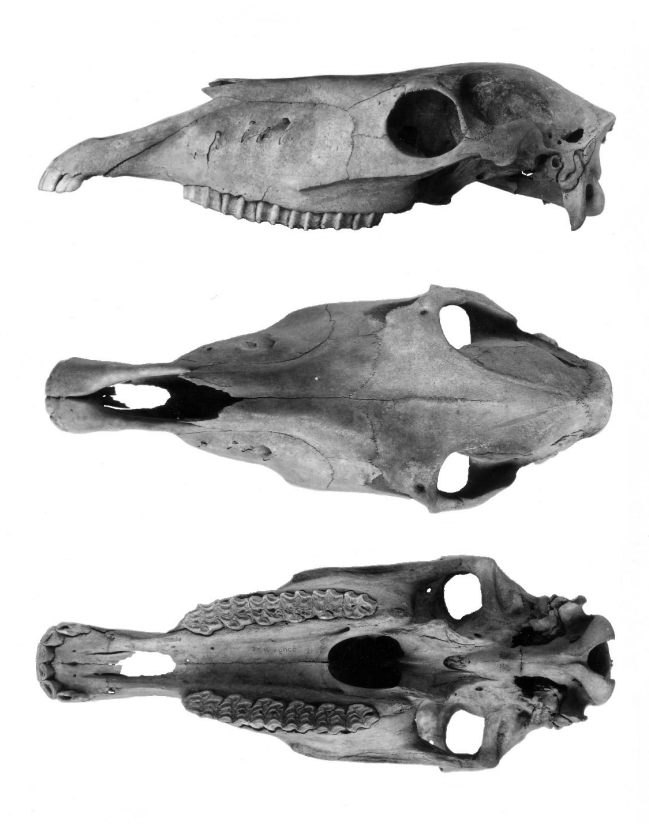

*Fig. 6. Left lateral (top), frontal (middle) and basal (bottom) aspects of an Early Hungarian horse skull from Koroncó, Hungary. Greatest length=488 mm (Bökönyi 1974: 285, Fig. 120).*

| **Measurement** | **Avar** | | | **Hungarian** | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **n** | **B-P%** | **rank sum** | **n** | **B-P%** | **rank sum** | **U** | **Z** | **p-level** |
| **A-P** | **29** | **109.3** | **887** | **48** | **111.1** | **2116** | **452** | **-2.565** | **0.010** |
| Eu-Eu | 16 | 22.7 | 428.5 | 39 | 23.2 | 1112 | 292.5 | -0.361 | 0.718 |
| Ect-Ect | 37 | 42.9 | 1544 | 50 | 43.6 | 2284 | 841 | -0.721 | 0.471 |
| Ent-Ent | 19 | 30.3 | 494.5 | 37 | 30.4 | 1102 | 304.5 | -0.813 | 0.416 |
| B-St | 31 | 46.6 | 1060 | 39 | 46.4 | 1425 | 564 | -0.479 | 0.632 |
| St-P | 32 | 53.6 | 1119 | 44 | 53.6 | 1807 | 591 | -1.189 | 0.235 |
| Ic-Pm | 29 | 19.8 | 1041 | 45 | 19.9 | 1734 | 606 | -0.515 | 0.607 |
| I-I | 30 | 14.1 | 990.5 | 38 | 14.5 | 1356 | 525.5 | -0.550 | 0.583 |
| B-O | 24 | 7.8 | 725.5 | 45 | 8.0 | 1690 | 425.5 | -1.443 | 0.149 |
| **$P^{2-4}$** | **31** | **18.3** | **935.5** | **45** | **19.4** | **1991** | **439.5** | **-2.727** | **0.006** |
| $M^{1-3}$ | 31 | 16.1 | 1019 | 38 | 16.3 | 1396 | 523 | -0.796 | 0.426 |

*Fig. 7. Mann-Whitney U Test of differences between relative measurements (B–P%) by period.*

| B-P% | A-P | Eu-Eu | Ect-Ect | Ent-Ent | B-St | St-P | Ic-Pm | I-I | B-O | $P^{2-4}$ | $M^{1-3}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Age** | 0.069 | -0.011 | **0.301** | 0.133 | -0.231 | 0.102 | -0.066 | -0.073 | *-0.357* | *-0.391* | -0.187 |
| **A-P** | 1.000 | 0.206 | **0.327** | **0.284** | 0.154 | 0.076 | **0.270** | 0.164 | **0.281** | -0.091 | 0.004 |
| **Eu-Eu** | | 1.000 | **0.392** | 0.096 | -0.028 | 0.060 | -0.087 | 0.249 | **0.375** | 0.205 | **0.448** |
| **Ect-Ect** | | | 1.000 | **0.534** | 0.061 | -0.005 | 0.005 | **0.348** | 0.222 | 0.057 | 0.015 |
| **Ent-Ent** | | | | 1.000 | 0.153 | 0.211 | 0.217 | -0.078 | 0.099 | -0.222 | -0.231 |
| **B-St** | | | | | 1.000 | *-0.693* | *-0.275* | 0.012 | **0.268** | 0.188 | 0.159 |
| **St-P** | | | | | | 1.000 | 0.402 | -0.021 | -0.126 | -0.119 | -0.009 |
| **Ic-Pm** | | | | | | | 1.000 | -0.023 | 0.074 | *-0.396* | *-0.355* |
| **I-I** | | | | | | | | 1.000 | 0.216 | **0.480** | **0.220** |
| **B-O** | | | | | | | | | 1.000 | **0.254** | 0.068 |
| **$P^{2-4}$** | | | | | | | | | | 1.000 | **0.546** |

*Fig. 8. Pairwise Spearman rank order correlations between cranial proportions (B–P%). Correlations significant at the p≤0.05 level are marked by boldface (+) and framed italics (-) respectively.*

### *Age related cranial proportions*

Relationships between the measurements expressed relative to basal length (B–P%) were studied calculating pairwise Spearman rank order correlations (Fig. 8).

Significant negative correlations were indeed found between age and the length of the premolar row (as well as the relative length of the *foramen magnum*). Meanwhile, the forehead becomes relatively wider with age as is suggested by the positive correlation between the percentage of greatest forehead breadth (Ect–Ect) and age.

The correlation matrix in Fig. 8 revealed additional, statistically significant correlations of interest. These were redefined for the purposes of synthetic interpretation using a factor analysis with Varimax rotation.

### *Interrelationships between cranial proportions*

The factor analysis based on the rank correlation matrix in Fig. 8 resulted in two factors (latent root>1). Although at this level, the variables available for study encompass only 43% of the total variance, the results can be used to outline relationships between groups of cranial proportions (Fig. 9). The clustering between these proportions is shown in Fig. 10 in the plane defined by the two factors.

The first factor is clearly age related, juxtaposing viscerocranium proportions that increase (diastema and palatal lengths, i.e. Ic–Pm and St–P) with age with those whose relative length decreases (tooth row lengths and B-St). The increase of [non-dental] longitudinal measurements in the viscerocranium is an amply documented phenomenon in mammalian ontogeny (e.g. Bartosiewicz 1980, 22). When contrasted to these evidently age dependent skull proportions, the slight broadening of forehead observed in Fig. 8 becomes insignificant.

The second factor represented proportions related to overall size (esp. A–P and breadths), all correlated with each other, but theoretically independent of the groups most determined by age. On the basis of Fig. 10, four groups of cranial proportions could be visually distinguished, as marked by codes 1 to 4 in the third column of Fig. 9.

| B-P% | Factor 1 Age | Factor 2 Size | Measurement group code |
|---|---|---|---|
| Ic-Pm | **0.586** | 0.264 | 4 |
| St-P | **0.509** | 0.200 | 4 |
| Age | **0.461** | 0.121 | – |
| Ent-Ent | 0.358 | **0.603** | 1 |
| A-P | 0.102 | **0.637** | 2 |
| Ect-Ect | 0.000 | **0.808** | 1 |
| Eu-Eu | -0.338 | **0.591** | 1 |
| B-O | -0.378 | **0.498** | 2 |
| I-I | -0.422 | **0.443** | 1 |
| B-St | *-0.514* | 0.061 | 3 |
| $M^{1-3}$ | *-0.675* | 0.098 | 3 |
| $P^{2-4}$ | *-0.796* | 0.071 | 3 |
| Latent root>1 | 2.784 | 2.314 | |
| Percentage explained | 23.201 | 19.284 | |

*Fig. 9. Factor loading matrix showing the relationships between cranial proportions.*

### *Phenotypic differences revisited*

It was hoped that by comparing groups of measurements whose proportions are least correlated with age (Groups 1 and 2), craniometric differences between Avar and Early Hungarian horses could be more easily pinpointed.

Absolute measurements thus selected were converted

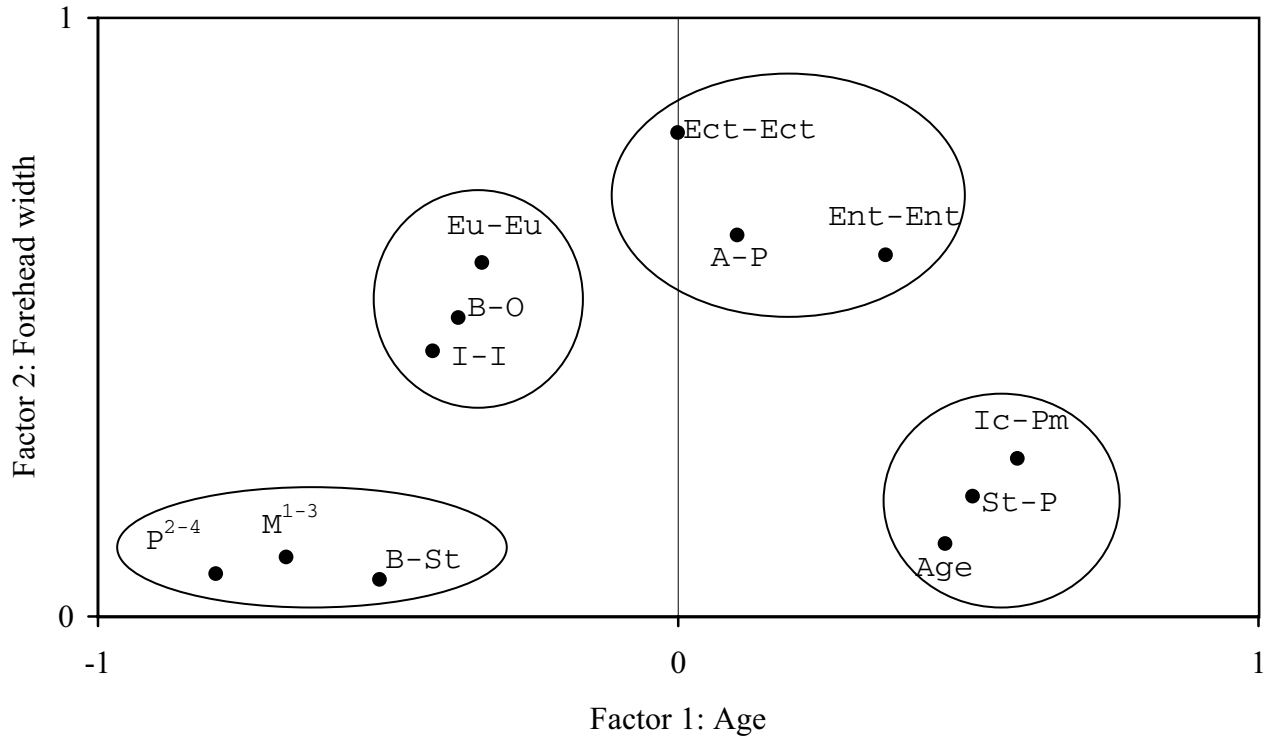


*Fig. 10. The configuration of cranial proportions (% of B–P) in the plane defined by the two factors.*

into variability size indices (VSI) as defined by Uerpmann (1979). This method of standardization was developed to compensate for the small number of measurements taken on fragmented skulls by making the direct comparison of several measurements possible.

Each individual measurement of the archaeological material was expressed as a standard score of the mean value and standard deviation of the respective measurement in the pooled Przewalski horse sample (Fig. 2; n=10). The resulting standard scores, representing each archaeological measurement (converted into conventional VSI values by multiplication with 25), made the comparison between Avar and Early Hungarian horse skulls possible against the background of Przewalski horses as a common standard.

Comparisons were carried out using correlated measurements (i.e. within Groups 1 to 4). It is at this point that better preserved skull dimensions (as shown by percentages in Fig. 1) became somewhat over-represented in calculations. In spite of all these targeted manipulations, Mann-Whitney U tests for measurement groups revealed no significant differences between the VSI scores of Avar and Early Hungarian horse skulls (Fig. 11).

Group 2 (in Fig. 9), characterized by the smallest (although non-significant) p-value was selected for the detailed study of size indices. VSI scores calculated for basal length, greatest skull length and the length of the *foramen magnum* were plotted against the standard interval represented by Przewalski horses in Fig. 12.

Most individual size indices of both Avar and Early Hungarian horses fall below the mean of pooled Przewalski horses. As mentioned before, the greater number of data representing the Hungarian Conquest Period results from the better preservation of measurements in this sub-sample (Fig. 1).

Both resulting curves reveal a certain degree of bimodality that could be most easily attributed to sexual dimorphism. This bimodality is better expressed and more symmetric in the skulls of [older] Avar horses. Although differences between stallions and mares were not significant in a formal statistical sense (Fig. 2), the smaller group of measurements in both samples may be interpreted as those of mares, while the larger seems to correspond to stallions and possibly geldings in both periods.

Finally, the skewed curve of Early Hungarian horse skulls, including several index values below -100 of the Przewalski standard reference sample, may be explained by the aforementioned greater contribution of young i.e. small individuals to this sub-sample.

Even in the absence of formal statistical parameters, Fig. 12 supports the impression that the few morphometric differences established between Avar and Early Hungarian horse skulls may be resulting from the differential age structure and sex composition of the two chronological sub-samples.

| Measurements | Avar | | Hungarian | | | | |
|---|---|---|---|---|---|---|---|
| | n | rank sum | n | rank sum | U | Z | p-level |
| Group 1 | 128 | 20028 | 168 | 23928 | 9732 | -1.398 | 0.162 |
| Group 2 | 99 | 13109 | 145 | 16781 | 6196 | -1.813 | 0.069 |
| Group 3 | 122 | 14560 | 124 | 15821 | 7057 | -0.909 | 0.364 |
| Group 4 | 78 | 7075 | 91 | 7290 | 3104 | -1.403 | 0.161 |

*Fig. 11. Mann-Whitney U test of differences between periods by measurement groups defined in Fig. 8.*

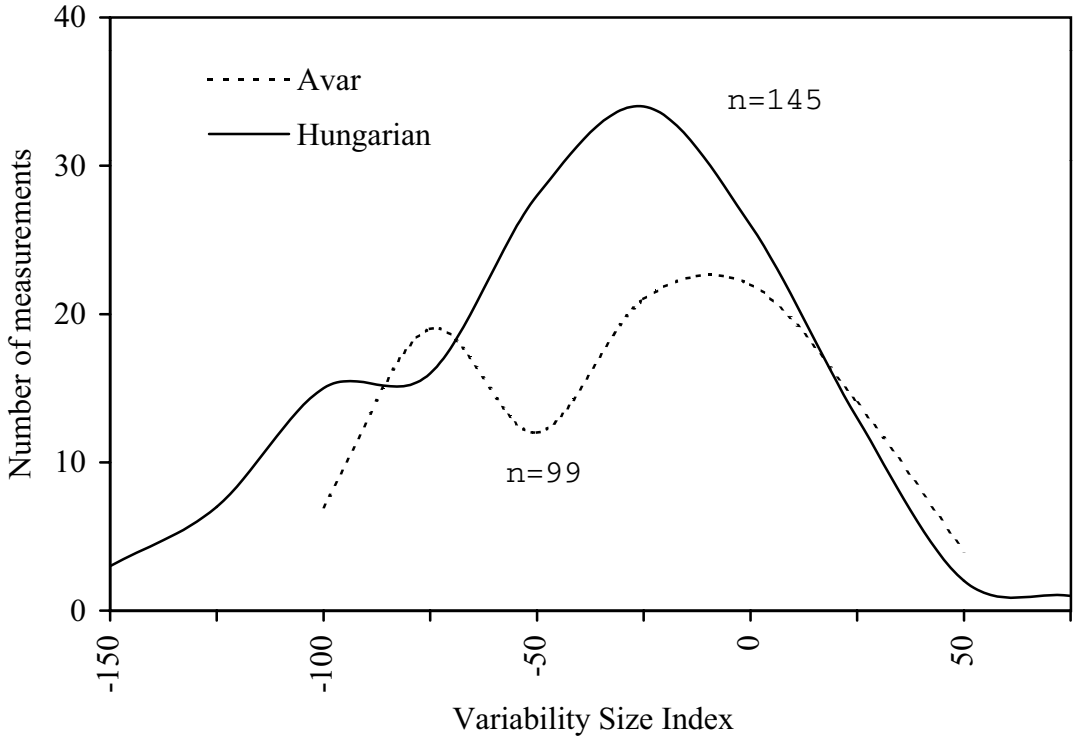


*Fig. 12. The distribution of Group 2 measurements plotted against the standard of pooled Przewalski mares and stallions.*

***Age differences revisited***

Indications that the only meaningful difference between Avar and Early Hungarian horses occurred in the length of the premolar row, inspired the estimation of ages for the pooled Avar and Early Hungarian sample available for study. As could be expected from the descriptions by Lundholm (1947), the linear regression equation calculated for the 53 individuals with *both* known dental ages and measurable premolar rows was supported by a significant but negative linear correlation (Fig. 13).
Age estimates calculated for individuals whose premolar rows were available for study, turned out to have been statistically different between the two chronological sub-samples (Fig. 14).

This difference supports the idea that some craniometric differences between Avar and Early Hungarian horses may indeed originate from the different age structures of the two chronological sub-samples available for study where the Avar horses tend to be older by more than one year than the horses placed in Early Hungarian graves.

***Relative forehead breadth***

The percentual proportion (B–P%) of greatest forehead breadth (Ect–Ect) was found to be only weakly correlated with age (c.f. Figs 8 and 9). When decimal logarithms of the two measurements are plotted against each other, they indeed display very similar trends in both chronological sub-samples, and their regression parameters do not significantly differ from each other Fig. 15; Fig. 16). In fact, the slopes (b) of the two resulting regression

| Dependent variable | n | r | p-level of r | Regression equation | p-level of b |
|---|---|---|---|---|---|
| $P^{2-4}$ length, mm | 53 | -0.370 | 0.05 | y=31.158-0.263x | 0.04 |

*Fig. 13. Age-dependent decline in the length of the upper premolar row ($P^{2-4}$).*

| | Avar | | | Hungarian | | | t-value | d.f. | p-value |
|---|---|---|---|---|---|---|---|---|---|
| | n | mean value | standard deviation | n | mean value | standard deviation | | | |
| Estimated age | 56 | 7.9 | 3.7 | 52 | 6.6 | 2.9 | 2.038 | 106 | 0.044 |

*Fig. 14. Differences between the estimated ages of Avar and Hungarian horses.*

| Group | n | r | p-level of r | Regression equation | p-level of b |
|---|---|---|---|---|---|
| Avar | 50 | 0.514 | 0.001 | y=-0.064+0.887x | 0.010 |
| Hungarian | 21 | 0.676 | 0.001 | y= 0.035+0.851x | 0.001 |

*Fig. 15. Relationships between basal length (B–P; x) and greatest breadth of the forehead (Ect–Ect; y) in the two chronological sub-samples*

equations, expressing the relative broadening of skull are almost identical with each other. They show that in both chronological sub-samples, a 10 mm increase in basal length would, on average, result in almost 9 mm broadening of the forehead. This, however, means that the forehead becomes relatively narrow with increasing size (the growth trend does not show isometry). This means that the exponential size index (ESI), developed by Matolcsi (1973b, 300), may have overemphasized the greater forehead breadth he observed in Avar horses. The visual appraisal of data points in Fig. 16, however, also shows that Early Hungarian horse skulls form the lower end of the size range within a uniform trend, while somewhat larger skulls are characteristic among Avar horses.

In fact, since two groups, those of smaller and larger skulls, may be visually distinguished in this graph (separated at the lg B–P»2.7 value), the trend seen in the distribution of VSI values in Fig. 12 (based on A–P and B–O) is confirmed by another pair of measurements (B–P and Ect–Ect) shown from a different aspect: smaller Early Hungarian horse skulls show a more asymmetric, skewed pattern owing to the presence of younger individuals. The configuration of larger Avar horse skulls, on the other hand, displays a more compact pattern of bimodality. The two groups, meanwhile, follow an identical trend of relative growth.

## Discussion and Conclusions

The analysis of cranial measurements yielded but a few metric differences between horses from the Avar and Hungarian Conquest Periods. Avar horse skulls tend to look somewhat larger and more robust, as also expressed from their general morphology. Figs 5 and 6 show three standard aspects each of a characteristic Avar Period horse skull (Pókaszepetk, Hungary; Bökönyi 1974, 281, Fig. 116), and of an Early Hungarian specimen (Koroncó, Hungary; Bökönyi 1974, 285, Fig. 120).

Morphological and metric differences, however, are not independent of the fact that skulls from the Avar Period originate from older animals than those representing Early Hungarian horses in Conquest Period burials. Metric analyses pointed to the *possible effect of age* on the previously observed craniometric differences between Avar and Early Hungarian horses:

– Elaborate classifications by Matolcsi (1982, 247–248, Fig. 83) based on the length of the upper tooth row are strongly influenced by the age structure of samples compared, and should, therefore be viewed with caution. This does not exclude the possibility of phenotypic differences in the length of the tooth row. These, however, may be most difficult to detect given the dominant pattern of age-related variability.
– The positive correlation (r=0.348; Fig. 8) between the percentual proportions of greatest skull breadth (Ect–Ect) and the greatest breadth of "snout" (I–I) is of special interest: Matolcsi (1982, 247) suggested

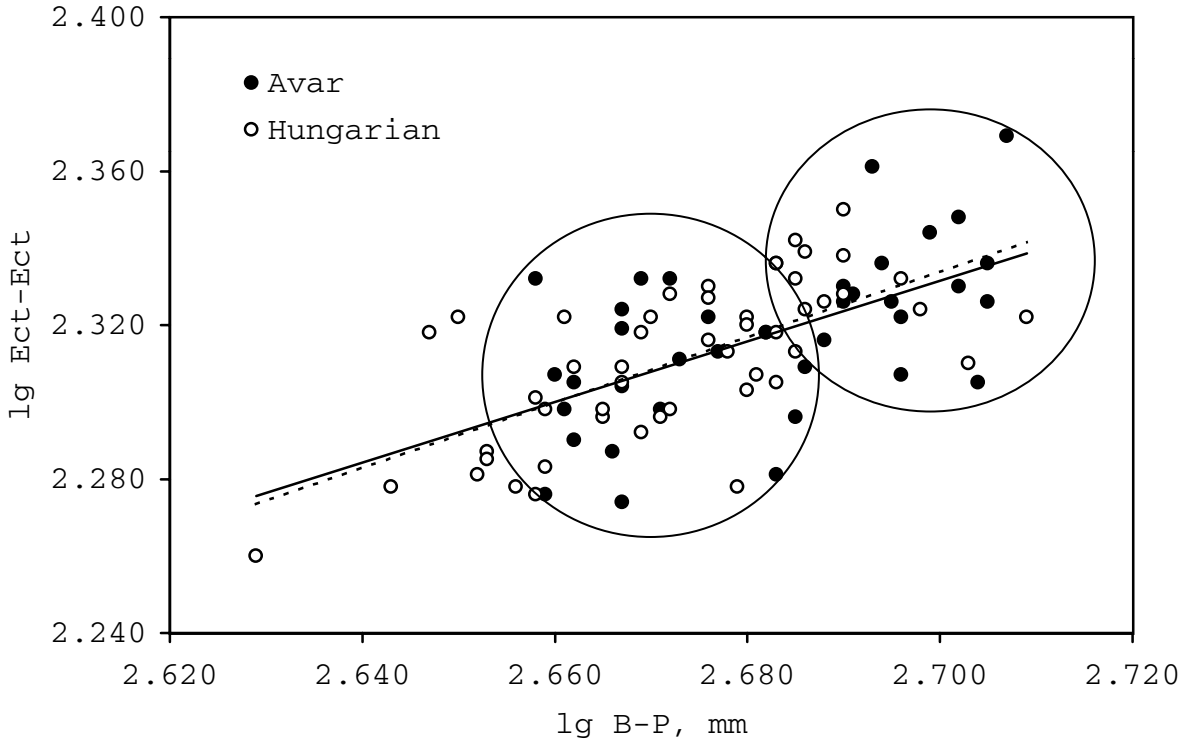


*Fig. 16. Allometric relationship between the basal length and greatest breadth of the forehead.*

that Avar horses had broader foreheads and narrower snouts than Early Hungarian specimens. Not only did the direct comparison of larger series of skull measurements fail to reconfirm this observation, but the high coefficient of correlation between these proportions (Fig. 8) reflects very little variation in this regard. (Moreover, the mean I–I/Ect–Ect ratio was identical, i.e. 0.333, in both chronological subsamples analyzed here: on average, the breadth of the snout tends to be one third of forehead breadth in both samples).

– Measurements most widely available, and thus included in this study, were ill-suited to express the difference in the protrusion of orbits, described as typical of Early Hungarian horses (Bökönyi 1974, 275). Bökönyi himself notes that this is not a "general difference". In addition, the position of orbits is also prone to age-related changes during ontogeny (Bartosiewicz 1980).

It would seem, therefore, that both groups of horses derive from similar stocks, kept and used in comparable ways. At the same time, however, it would be erroneous to interpret this functional/phenotypic similarity between horses as evidence of direct cultural continuity between the two historically and ethnically different groups of people. Horses have always been appreciated prestige items, ranging from highly prized royal presents to desirable war booty. Genetic homogeneity would have been increased by the well-known mobility of horse stocks as well as the continuous movement of horses between various steppe groups both inside and outside the Carpathian Basin. The manifestations of phenotypic variability are also influenced by the fact that Avar warriors seem to have been buried in the company of war horses that had functionally determined physical traits, including optimal age and size.

This is not to say, that distinctions would not become more evident using an improved set of data. The phenomena observed in this paper, therefore, need to be refined by:

– Being based on more detailed metric criteria as well as non-metric variables.
– Larger sample sizes facilitating finer chronological and regional sub-divisions within periods (within sample variability seems to significantly contribute to the morphometric overlap observed between the two gross chronological sub-samples summarized under the umbrella terms of "Avar" and "Early Hungarian").
– Comparisons with contemporary horse skulls from the Eurasian steppe, critical to our understanding of the horses used by both these historically significant peoples.

At this point, cultural differences seem better reflected in the way younger horses were sometimes interred in Early

Hungarian graves than by the cranial morphometry of the animals themselves. When the age and sex of animals are taken into consideration, several of the differences in shape may be attributed to the divergent compositions of the two chronological sub-samples. In general, mares are somewhat underrepresented in burials in the two studied periods. While the majority of Avar horses were killed in their prime (4–10 years), some Early Hungarian burials contained the remains of rather young individuals that could not yet be considered seasoned 'war horses'. The Hungarians therefore, may have practiced a form of burial sacrifice where it was chiefly important to place "a" horse in the grave. Among the Avars, on the other hand, it appears that it could have been the warrior's mount which was sacrificed at the time of burial. Thus, cranial differences between the two groups of horses seem to be influenced by some form of divergent cultural practice.

*Acknowledgments*

Grateful thanks are due to Dr. Deborah Ruscillo who supported the presentation of this paper in the session entitled "*Ageing and sexing*" at the 9th Conference of ICAZ in Durham, UK. Thanks are due to my reviewers, Marie-Eve Brodeur and Ruth F. Carden who have improved the original manuscript by contributing valuable remarks. Cranial measurements of Przewalski horses were provided by the late István Takács of the Hungarian Agricultural Museum. Figs 5 and 6 have been reproduced after Bökönyi (1974) with permission by the publisher. The English text was revised by Dr. Alice M. Choyke. Last but not least, help by Kyra Lyublyanovics with image processing is also acknowledged here. I wish to acknowledge the travel grant awarded to me by the Institute for Aegean Prehistory for travel to the ICAZ meetings in Durham.

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*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 216–226*

# 14. Documenting the Channel Catfish Population Exploited by the Prehistoric Inhabitants of the Station-3-avant Site at Pointe-du-Buisson, Southern Québec (Canada)

*Marie-Eve Brodeur*

*The faunal assemblages from two of the Pointe-du-Buisson sites have been analysed. They show that channel catfish (*Ictalurus punctatus*) was the main species exploited by the prehistoric occupants of these sites (Cossette 1995; Courtemanche 2003). The channel catfish bone assemblage from the Station-3-avant site, also located on Pointe-du-Buisson, has been analysed osteometrically. Fork length and age distributions were reconstructed and reveal a pattern of selection of these ancient fishermen, as well as an important change in their exploitation strategy through time, resulting in an intensification of the exploitation of that catfish resource.*

## Introduction

The Station-3-avant site is located on Pointe-du-Buisson along the St. Lawrence River, about 30 km southwest of Montréal, in Southern Québec (Fig. 1). The area is flanked by some important rapids which made portage necessary throughout prehistory (Fig. 2). The Station-3-avant site is characterized by short intermittent occupations during the 5,000 years of human presence documented at Pointe-du-Buisson. The site was most intensively occupied during the Early Middle Woodland Period and, to a lesser degree, during the Late Woodland Period and Late Archaic Period (Fig. 3) (Clermont 2001). The locale offers a rich ichthyofauna including spawning sites in rapid and slow waters. It has been recognised since at least the mid-19th century as an exceptional fishing spot from spring thaw ice to late autumn (Montpetit 1872).

The faunal assemblages from two of the Pointe-du-Buisson sites have been analysed and the results indicate that channel catfish (*Ictalurus punctatus*) was the main species exploited by the prehistoric occupants of these sites (Cossette 1995; Courtemanche 2003). In this research, I have tried to document the exploitation of this particular species using an osteometric approach. Osteometry can provide an examination of the selection criteria used by ancient fishermen. It can be used to recognize the methods of capture practiced during the past, and it also allows the recognition of different exploitation strategies through time. Station-3-avant, the richest of the Pointe-du-Buisson sites and certainly the one which has the longest occupational record, offers an adequate collection for that kind of study.

In this chapter, I will present the results concerning: 1) the selection of prey size and age and, 2) changes in exploitation strategies through time. But I shall first discuss the biology of the channel catfish and the methodology employed in this study.

## Biology of the Channel Catfish

The geographical distribution of the channel catfish is quite extensive; the species is found in all medium to large freshwater bodies of Eastern North America (Hubbs and Lager 1958). In the province of Québec, it is the largest species of the *Ictaluridae* family (Fig. 4).

Channel catfish can survive in several different habitats, an indication of their high degree of adaptability. Habitat selection is influenced by: 1) different behaviours between age classes as a function of their feeding habits, 2) the abundance of resources in the region, which may necessitate the exploitation of multiple habitats during

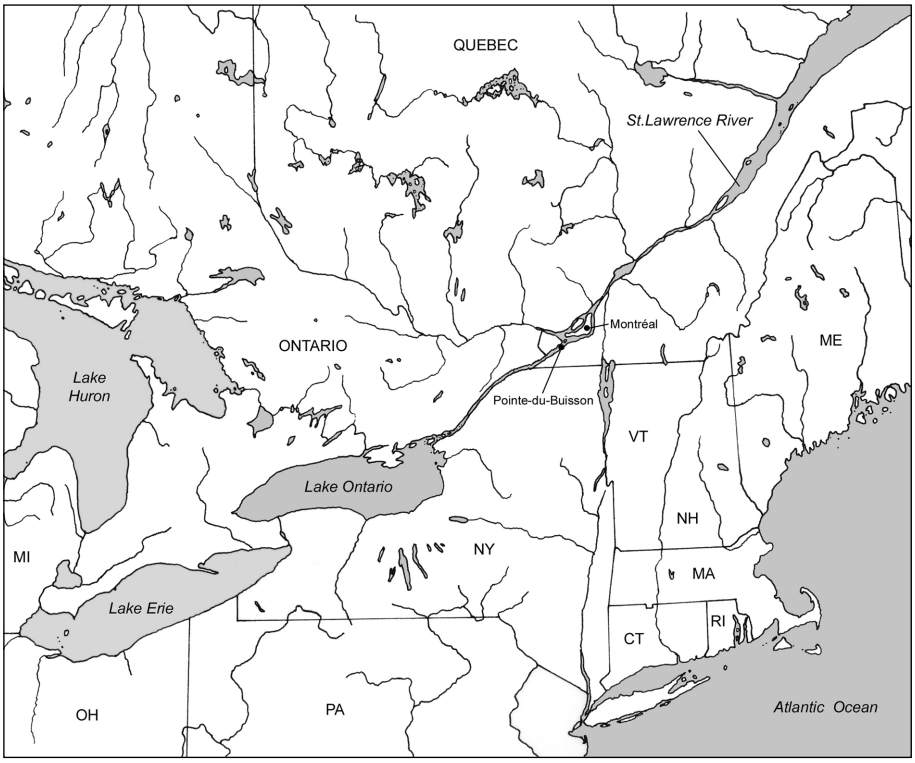



*Fig. 1. Location of the Pointe-du-Buisson.*

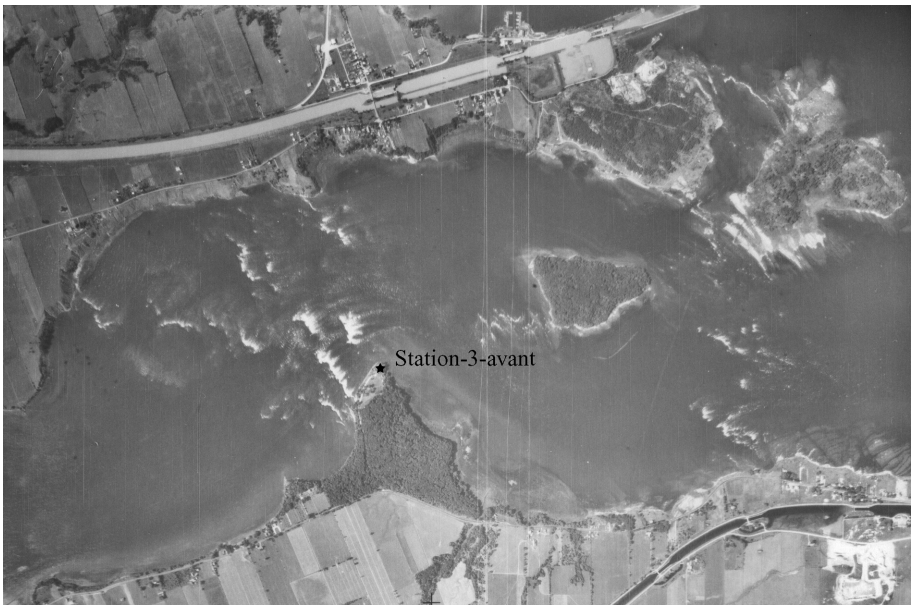



*Fig. 2. Pointe-du-Buisson and its rapids (1926).*

the year, 3) seasonal variation associated with the water temperature and spawning behaviour and, 4) the survival behaviour of the young as they must avoid predators such as other larger fish, including mature channel catfish (Bailey and Harrison 1948; Latour *et al.* 1980).

It is common for individuals of this species to move several kilometres in a couple of days or hundreds of kilometres in a year. Migration studies undertaken in the United States have recognized some life-long patterns in which juveniles are found in tributaries while young and

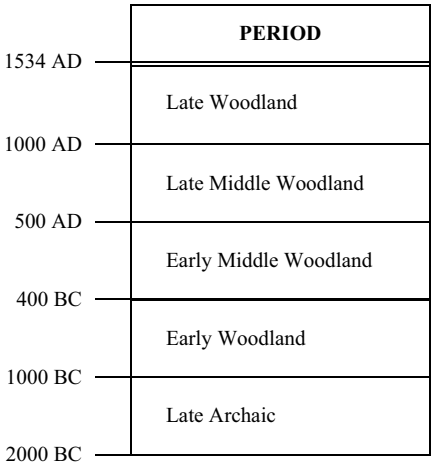



*Fig. 3. Chronological sequence of the Station-3-avant site.*

mature individuals stay in the main river (e.g. Dames *et al.* 1989). The low numbers of young and juveniles captured by biologists in the province of Québec do not allow the identification of such a pattern with regards to the St. Lawrence River. The great attachment revealed by adult channel catfish to their summer homing sites leads researchers to believe that the waters of Pointe-du-Buisson probably supported a population of channel catfish almost from the spring rise in water level to late in the fall season (Magnin and Beaulieu 1965; Montpetit 1872). The rich and diversified environment of Pointe-du-Buisson (Clermont and Chapdelaine 1982; Cossette 1995) allows the fish to exploit tightly clustered areas for their resting, feeding and spawning activities.

The channel catfish is largely, but not exclusively, a nocturnal feeder active mostly from sunset to midnight. Changes in activity are often accompanied by changes in habitat. The fishermen take advantage of the predictable movements involved in the transition. Day resting sites are often located in pits under rapid and deep waters, while their feeding sites vary depending on food availability (Brown *et al.* 1970; Davis 1959; Stevens and Tiemier 1961). In general, the young (under 300 mm long) are insectivorous, the juveniles and young adults (from 300 to 450 mm) are omnivorous and adults (greater than 450 mm) are mostly piscivorous (Smith 1974).

The spawning period extends from the end of June to the beginning of July in water temperatures between 20.6° and 23.3°C (Smith 1974). In our study area, sexual maturity for males occurs at about 7 to 8 years of age (318–343 mm fork length) and at 6 to 7 years of age (309–334 mm fork length) for the females (Bélanger 1989). Later on, the males become slightly larger than the females because they benefit from one more year of growth before investing energy in the production of their gonads, while females do not. However, channel catfish are not sexually dimorphic for length (Appleget and Smith 1951; Bélanger 1989; Elrod 1974; Gerhardt and Hubert 1991; Jearld 1970; Lorantas 1982; Smith 1974). Accordingly, it is acceptable to apply a single equation for growth rates even if we do not know the sex of the specimens, as is often the case with archaeological assemblages.

The prehistoric inhabitants of Pointe-du-Buisson probably favoured the exploitation of the channel catfish for various reasons, such as 1) the good yield per capture that this species provided, 2) its gregariousness and its frequent moves which might have facilitated its capture, 3) its predictability as a result of its homing behaviour, 4) the fact that it can be easily conserved by smoking, but most importantly, 5) because of its high fat content. We know that Native Americans highly prized fat in their food sources, and channel catfish is among the fat-richest fish species in Eastern North America.

## Methodology

My analyses used osteometric measurements taken on five anatomical elements of the channel catfish assemblage recovered from the Station-3-avant site. Based on data obtained from other sites of Pointe-du-Buisson, I chose skeletal elements that were most often complete (i.e. unfractured), and that were also most easily identified to the species level. These are the dorsal and pectoral spines, the angular, the dentary, and the basioccipital. These are also anatomical elements frequently used in fish osteometrical analyses (e.g. Desse and Desse-Berset 1987–96; Morales and Rosenlund 1979). I used standard measurements adapted to the skeletal morphology of the channel catfish and added others which can be made on fragmentary material (Fig. 5). Thus, the total number of measured specimens were increased. All measurements were taken using a digital calliper (estimated margin of error: 0.05 mm).

Biological and osteological measurements have been taken on present day fish from the reference collection. This collection is composed of 32 channel catfish of various sizes. It was used to establish correlations between biological (length, weight and meat weight) and osteological data. To these data, I added those concerning the length, weight and age of some other 431 channel catfish generously provided by a biologist, Bruno Bélanger (1989), who conducted a study on the habitat, age and growth of the channel catfish from a site located less than 6.5 km from Pointe-du-Buisson, along the same river. Finally, I took bone measurements on 100 pectoral spines from Bélanger's specimens. This information complemented the data contained in the reference collection.

I tested four regression models to determine the one which gave the best predictive values for each estimation :

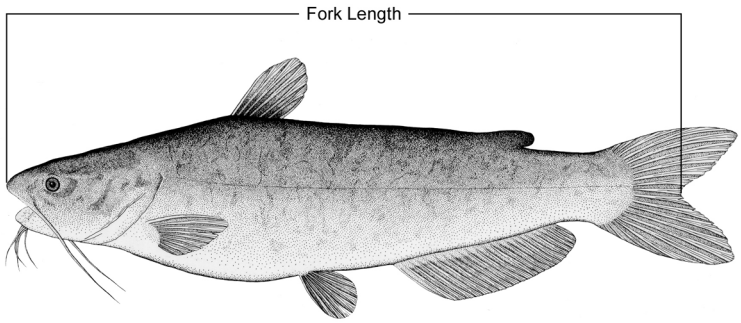



*Fig. 4. The channel catfish,* Ictalurus punctatus *(Bélanger 1989).*

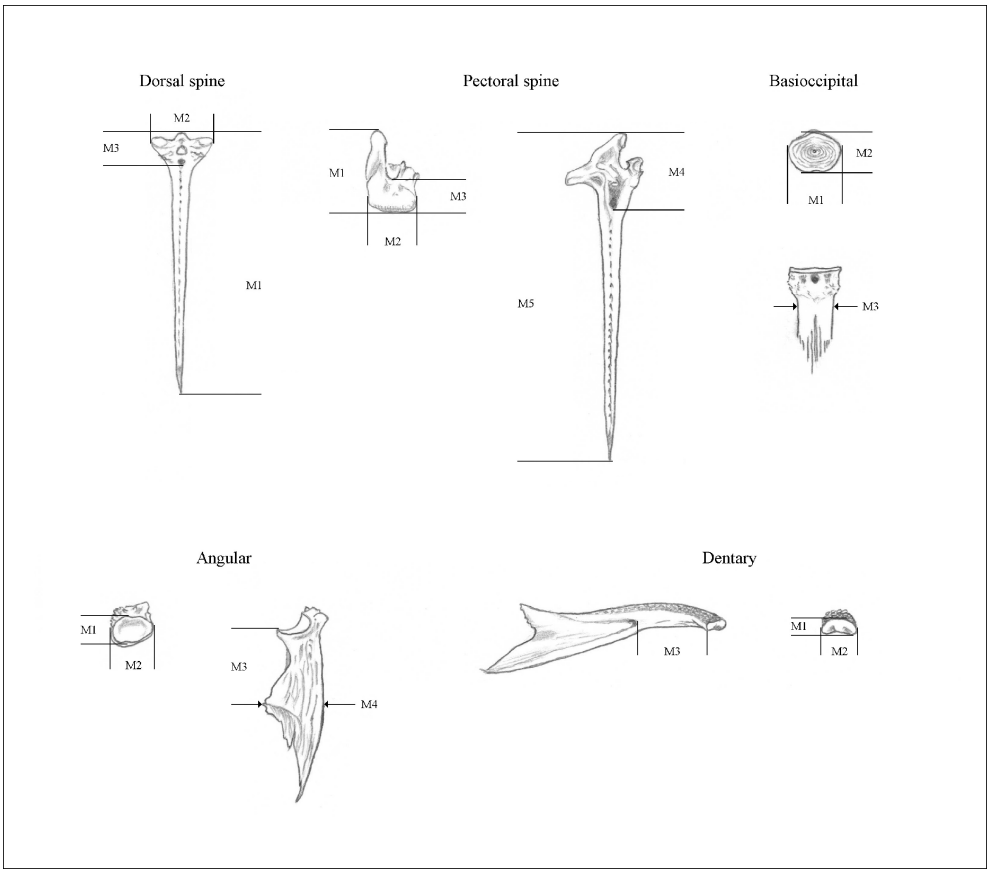



*Fig. 5. Bone measurements.*

Linear regression: Y = a + (b * X)
Logarithmic regression: (Ln) : Y = a + (b * Ln (X))
Power regression: Y = a * (X ** b)
S regression: Y = e ** (a + (b / X))

where **Y** represents the biological measurement to be estimated, **X** is the bone measurement, **a** is the Y-intercept, **b** is the slope, **Ln** is the natural logarithm ($\log_e$) and **e** is the basic value of the natural logarithm (~2.71828). I accepted regressions with an $r^2$ adjusted of at least 0,85 with a confidence level of 95% or more.

The archaeological collection analyzed is composed of 7,182 bones, 548 of which are dorsal spines, 2,058 are pectoral spines, 2,203 are angulars, 1,440 are dentaries, and 933 are basioccipitals. The minimum number of individuals (MNI) is 1,104; this calculation was based on the most abundant skeletal element: the right angular. In the assemblage, only the specimens on which at least

one measurement could be taken have been retained in my analyses. I applied the estimation equations established from the reference collection to the measurements taken on archaeological bones, and used the mean result for each bone.

The age of the individuals in the faunal assemblage was the most difficult estimation to make, partly because the 32 modern specimens of the reference collection were not aged. I tried to use Bélanger's (1989) data regarding age combined with the few measurements I took on the 100 pectoral spines of his collection. The results of the regression tests between age and these measurements did not prove to be statistically significant, so I searched for an alternative.

The channel catfish grows too slowly to use the length-frequency data; this creates overlaps between the distributions of age classes. As MacDonald pointed out, "The modes of the histogram are, clearly, poor indicators of the modes of the underlying theoretical distribution […]. Thus, any method based on modes or on the visual interpretation of probability plots will be subjective and unreliable, unless the components are as well separated […]." (1987, 373). He also underlined the fact that, "Age-at-length data, obtained by ageing all individuals in a subsample stratified by length, is a more promising approach for two important reasons: the problem of length bias in the sample is avoided; it is possible to put extra sampling effort into the longer lengths where, typically, overlap between age-groups is greatest" (MacDonald 1987, 372). The problem is that most individuals in the archaeological collection are larger in size than those in Bélanger's collection, so I used the same method as his. Thus, I used a regression between the fork length and age. The problem was that I could only apply that equation to estimated fork length. As a consequence, the results of the estimated ages are less accurate than if they had been estimated from a direct measurement on the bones. Moreover, the few specimens under 300 and over 600 mm in fork length in the reference collection accentuate this problem of reliability for these length categories. We should thus interpret the results as relative, considering that none provides the real ages of the captured fish on the Station-3-avant site. This ageing methodology is open to criticism, but I think that it is precise enough for the reconstruction of prehistoric exploitation strategies of the channel catfish population and it represents the best method available for estimating the ages of the fish captured at the site.

In this study, I was also interested in determining whether changes occurred in the exploitation strategies of channel catfish through time. The division of the archaeological deposits on Station-3-avant site into time periods is complicated by the fact that there was no visible stratigraphy: the cultural deposits, which varied from 12 to 55 cm in thickness, were ensconced in an apparently homogeneous alluvium with high organic content, which overlay a sterile clay layer. In spite of this soil uniformity, however, it is statistically possible to recognize the sequential deposition of cultural materials based on the frequency of chronologically diagnostic artifacts (Blais 1992; Clermont and Chapdelaine 1978; Morin 1998; Vernier 1999). Thus, I established a separation of the bones in three arbitrary levels that I compared with an analysis of variance (ANOVA) and pairwise comparisons based on the T-test method by least significant differences (LSD). For the sub-assemblages not normally distributed, I used the non-parametric Kruskal-Wallis test. The results of these tests combined with histograms of length and age per statistically differentiated level of the assemblage revealed some interesting tendencies over time.

## Results and Discussion

The average size of the channel catfish captured by the prehistoric inhabitants of the Station-3-avant site was estimated to be 541 mm (fork length) and 2,564 g (total weight), with an age-at-death of 17 years. However, size variation is great. Thus, the smallest specimen had 135 mm in fork length, 4 g in total weight (probably underestimated), and approximately one-and-a-half years old; whereas the biggest fish captured measured 944 mm in fork length, weighed 11,606 g and was 43 years old (Fig. 6). Such variations in size give the impression that almost all the size categories were present in the collection in proportion to their availability in nature. In fact, they were not evenly exploited by the prehistoric fishermen. Their main interest was for 16–17 year-old fish with a fork length of about 550 mm and a body mass of about 2,000 g and, to a lesser degree, for juveniles around 325 mm in length, 500 g in weight and 7–8 years in age (Fig. 7). Scrutiny of the frequency histograms by anatomical elements suggests that the primary targets of the prehistoric fisherfolk were the old mature individuals of the population and the juveniles, while the young mature channel catfish between 375 and 450 mm in fork length and 9 and 13 years in age were less frequently captured (Fig. 8).

It is noteworthy that each skeletal element generates different size and age groupings. Size frequencies estimated from the assemblages of dorsal and pectoral spines show a category of young channel catfish that seem to be more marginal with estimations established by angulars, dentaries and basioccipitals. Many factors can explain this phenomenon: 1) the more rapid allometric growth of these defensive structures which are proportionally larger than the rest of the skeleton for the young, and are thus more easily recovered on archaeological sites, 2) the differences in recovery rates where some elements are considered to be more diagnostic whatever their size, or, 3) the differential fragmentation of elements. If we put aside the young specimens of channel catfish captured, all the profiles of estimation

| | N | Range | Minimum | Maximum | Mean | Std. Deviation |
|---|---|---|---|---|---|---|
| Fork length (mm) | 6386 | 808.22 | 135.27 | 943.49 | 541.40 | 118.11 |
| Total weight (g) | 6405 | 11601.60 | 3.89 | 11605.49 | 2563.62 | 1545.27 |
| Age | 6386 | 42 | 2 | 43 | 17 | 6 |
| Valid N (listwise) | 6376 | | | | | |

*Fig. 6. Descriptive statistics of the total archaeological collection.*

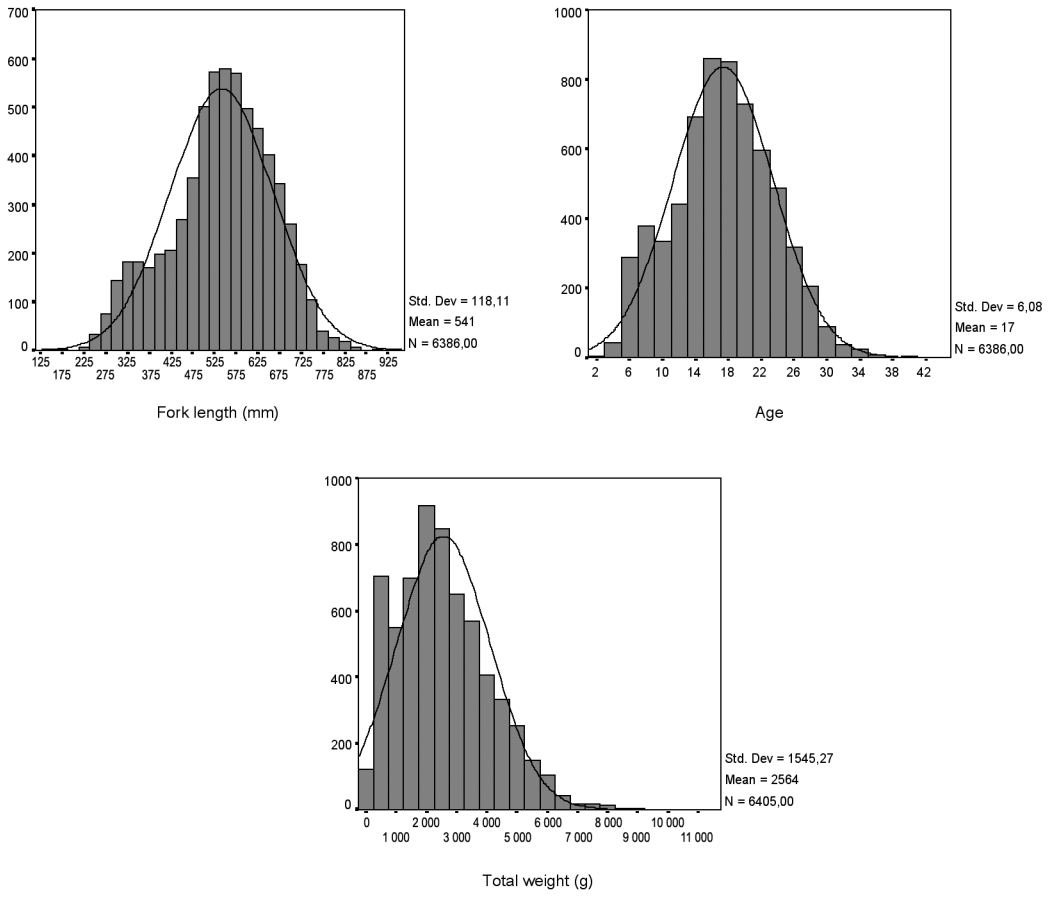



*Fig. 7. Reconstruction of fork length, total weight and age frequency distribution for the total archaeological collection.*

seem to be similar and suggest an exploitation of large fish where the mode is between 500 and 575 mm in fork length or between 15 and 18 years of age. In the assemblages containing the young individuals, the second mode is at 325 mm in fork length or between 6 and 8 years old.

The categories of length, weight and age that are most frequent in samples recovered for most biological studies of channel catfish in the region (Bélanger 1989; Magnin and Beaulieu 1965; Smith 1974) are generally those that are the less frequent in the archaeological assemblage (Fig. 9). Thus, the catch effort of these biologists resulted in recovered channel catfishes mostly having between 400 and 450 mm in fork length, between 750 and 1,000 g in total weight, and having an average age of 12 years (Bélanger 1989). The catching methods and the environment of the fishing station can skew the composition of the captured population, but we can nevertheless deduce firstly, that the channel catfish larger than 450 mm, having more than 1,000 g and being more than 13 years old are naturally less frequent in this environment and, secondly, that the channel catfish mostly captured by the biologists naturally represent the most numerous category within the mature population. Thus, we can identify a certain selectivity by the

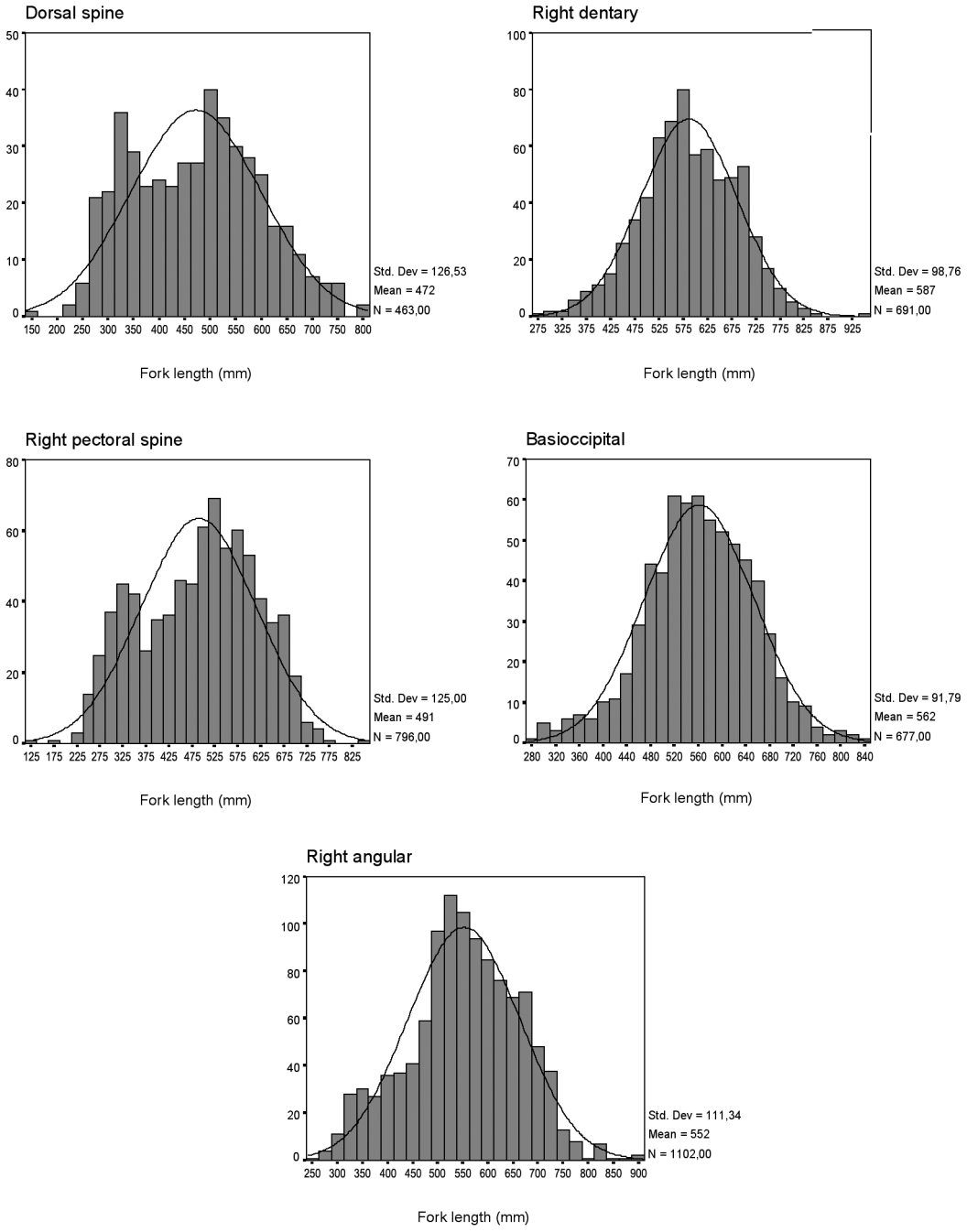



*Fig. 8. Reconstruction of fork length frequency distribution from the dorsal spine, the right pectoral spine, the right angular, the right dentary and the basioccipital.*

prehistoric fishermen who tended to neglect that fraction of the population and concentrated their efforts on the capture of juveniles (i.e. those between 5 to 8 years old) and mostly on fish having more than 14 years of age (i.e. the more productive catch per capture). These ancient fishermen were apparently well acquainted with the behaviour, habits and accessibility of the various sizes of channel catfish, but also the selectivity of their fishing gear. They were at some level opportunistic, because all sizes are present in the various chronological assemblages, but they are also characterized by an important selectivity based on the size of the prey that was more intensively exploited.

It also seems that channel catfish exploitation changed through time. As previously mentioned, I have defined three arbitrary chronological levels, where the middle one approximately corresponds to the main occupation period on the site: the Early Middle Woodland Period

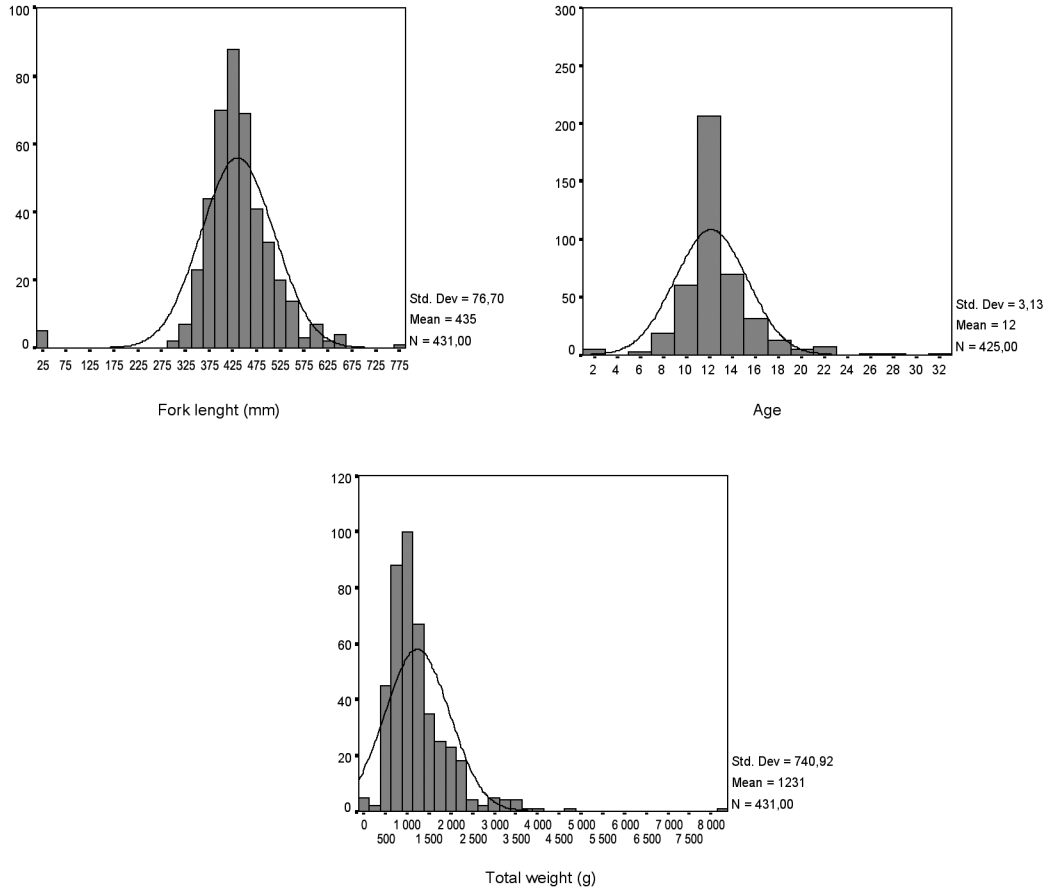



*Fig. 9. Fork length, total weight and age frequency distribution of channel catfish recovered by Bélanger's biological study.*

(400 BC to 500 AD). However, we cannot precisely associate any particular exploitation strategy of channel catfish with any of the specific time periods identified at the site. Comparing the results from each of the three arbitrary levels can only allow the identification of some very general tendencies through the 4,500 year span of prehistoric occupation of the site.

What can be noted is that, in general, the mean length of the captured channel catfish gradually declined through time (Fig. 10). The most revealing result concerns the length and age illustrated by the frequency histograms per level. Thus, we see a general tendency of a catch reduction of the biggest specimens of the population and an increase of the proportion of juveniles. In the deepest and oldest level, the exploitation was oriented toward large adults having between 500 and 600 mm in fork length and being 15 to 20 years old. The larger and the smaller individuals were not totally neglected but were not as intensively sought. In the middle level, associated to the Early Middle Woodland Period, we see a broadening of the prey size most intensively exploited as larger specimens having between 500 and 700 mm in fork-length were then included. The low intensity exploitation of juveniles (around 300 mm, 6–7 years) seemed to have continued, and may even be said to have slightly increased. In the last and most recent level, we see a marked decrease in the importance of individuals having more than 600 mm in fork length and over 20 years of age. The exploitation was more orientated toward the capture of individuals having between 500 and 550 mm in fork length, accompanied by an increase of juveniles (Fig. 11).

The great number of specimens present in the last level entitles us to subdivide it into three sub-levels. Interestingly, the same tendencies have been identified between those sub-levels. Thus, we observe a constant increase of the relative importance of juveniles (Fig. 12). At the same time, we see a decrease in the earliest sub-level of fish longer than 600 mm combined with an increase of fish between 500 and 600 mm, which is succeeded in the second sub-level by another focus around fish of 500-550 mm and a decrease of fish longer than 650 mm. At the most recent sub-level, the exploitation seems to have targeted many different cohorts (300 ± 25 mm, 400 ± 25 mm, 550 ± 25 mm and, less importantly, 625 ± 25 mm) with approximately the same intensity,

**ANOVA**

Fork length (mm) per level

| | Sum of Squares | df | Mean Square | F | Sig. |
|---|---|---|---|---|---|
| Between Groups | 370554.3 | 6 | 61759.06 | 4.151 | .000 |
| Within Groups | 22453286 | 1509 | 14879.58 | | |
| Total | 22823841 | 1515 | | | |

Fork length (mm) per level

| | N | Mean | Std. Deviation | Std. Error | 95% Confidence Interval for Mean | | Minimum | Maximum |
|---|---|---|---|---|---|---|---|---|
| | | | | | Lower Bound | Upper Bound | | |
| 35-clay | 29 | 548.76 | 108.08 | 20.07 | 507.65 | 589.87 | 350.63 | 815.58 |
| 30-35 cm | 54 | 556.26 | 121.88 | 16.59 | 523.00 | 589.53 | 273.12 | 735.59 |
| 25-30 cm | 223 | 545.43 | 124.41 | 8.33 | 529.01 | 561.85 | 268.58 | 910.73 |
| 20-25 cm | 422 | 532.75 | 118.38 | 5.76 | 521.43 | 544.08 | 237.28 | 840.37 |
| 15-20 cm | 562 | 519.20 | 125.14 | 5.28 | 508.84 | 529.57 | 135.27 | 842.51 |
| 10-15 cm | 194 | 510.87 | 120.13 | 8.62 | 493.86 | 527.88 | 268.30 | 758.83 |
| 0-10 cm | 32 | 461.63 | 118.11 | 20.88 | 419.05 | 504.21 | 239.19 | 649.59 |
| Total | 1516 | 526.44 | 122.74 | 3.15 | 520.25 | 532.62 | 135.27 | 910.73 |

*Fig. 10. ANOVA and descriptive statistics of fork length on the total assemblage per arbitrary levels.*

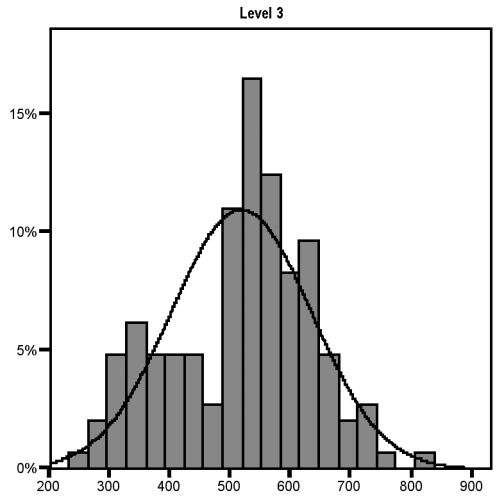
but this observation is based on a limited number of specimens (N=44) and must treated with caution.

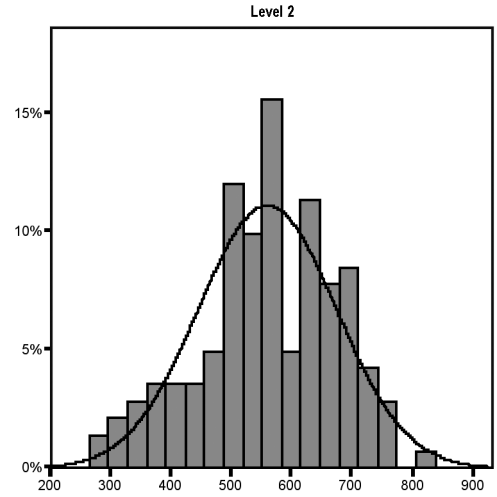
## Conclusion

This osteometric study shows that the prehistoric fishermen who occupied the Station-3-avant site were quite selective regarding the size of the channel catfish they captured. It also appears that the size frequencies of the captured fish were not constant through time. Our data suggest the existence of an intensification process in the exploitation of the channel catfish manifested by the adoption of two distinctive and successive strategies. During the Early Middle Woodland Period, the inhabitants of the Station-3-avant site broadened the size range of the older mature channel catfish exploited, corresponding to the more profitable fish in meat weight per catch. Later, they gradually begun to add the size category that was previously marginal in the captured population, namely the juveniles. Maybe the diminution of large size captures (more than 700 mm fork length) was a result of some fishing pressure reducing the life expectancy of the population of channel catfish near the site or a result of some change in the water temperature. In either case, the inhabitants of the site then had to change their exploitation strategies. But in fact, I believe that neither the exploitation pressure, nor the possible water temperature changes were important enough to produce that modification in the channel catfish population. Thus, it seems that we must look elsewhere for the reason of the decline of the larger specimens. Moreover, why did they choose to exploit the juveniles instead of the young mature channel catfishes? Part of the answer probably lies in the fishing environments that were probably different from those sampled by Bélanger (1989) and other biologists, where different fractions of the population are dominant. Many avenues should be considered and investigated in the future that might explain these choices, including the accessibility of the specific environments where the different categories of size are usually found, the methods of capture that were used, and some cultural choices which may not have necessarily aimed at an economic optimization of the catching efforts.

*Acknowledgements*

I would like to thank Norman Clermont, Christian Gates St-Pierre, Claire St-Germain and Michelle Courtemanche for their comments on the first version of this paper, as well as André Costopoulos for the English editing of the first version. The comments from two reviewers, Simon Davis and Sophie Louguet, and those from Richard Cooke were also very helpful. Finally, I am grateful to the Alma Mater foundation of Université de Montréal and to the ICAZ organizers for their financial support, including a travel grant awarded from the Institute of Aegean Prehistory, which allowed me to attend the conference at which a first version of this paper was presented.



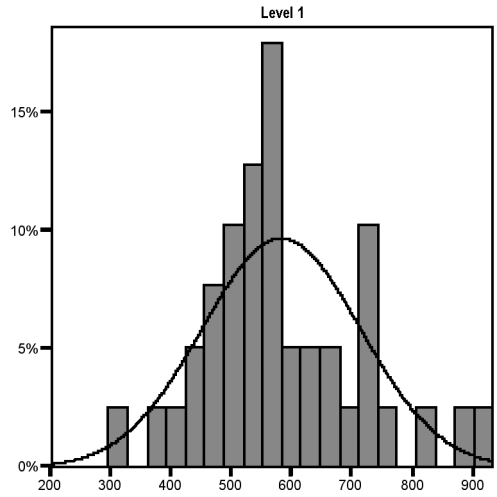
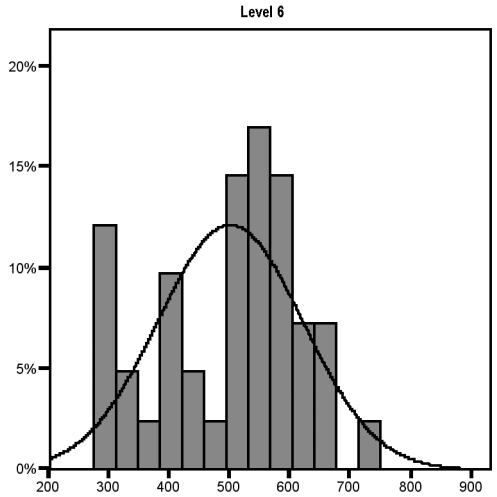
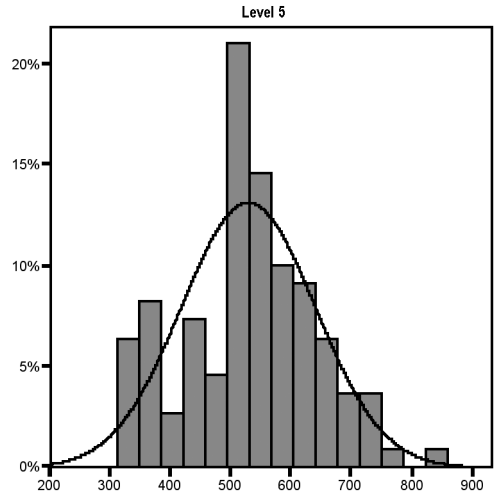




*Fig. 11. Histogram of fork length reconstructed from right angular per level (1: early; 2: middle; 3: late).*



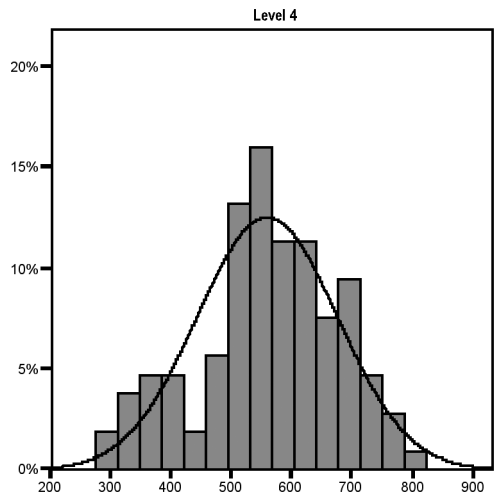




*Fig. 12. Histogram of fork length reconstructed from right angular for the sub-levels of the level 3 (4: bottom of level 3; 5: middle of level 3; 6: top of level 3).*

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*9th ICAZ Conference, Durham 2002*
*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 227–236*

# 15. Epiphyseal Fusion in the Postcranial Skeleton as an Indicator of Age at Death of European Fallow Deer (*Dama dama dama*, Linnaeus, 1758)

*Ruth F. Carden and Thomas J. Hayden*

*Sets of postcranial skeletal elements (scapula, humerus, radius, ulna, metacarpal, pelvis, femur, tibia and metatarsal) were prepared from 118 male and 92 female fallow deer from an enclosed population. All individuals were of known age. Specimens ranged in age from neonates to 15 (male) or 22 (female) years of age. All epiphyseal regions of the selected bones from each animal were classified into three categories depending on the degree of closure of the epiphysis and/or visibility of the suture line. The ontogenesis of closure of 28 different epiphyses/sutures is summarised and a protocol for estimating the age of archaeological or recent skeletal specimens is presented together with an evaluation of the accuracy and precision of the procedure.*

## Introduction

Artiodactyl fossils are more prevalent, widespread and preserved in many late Pleistocene deposits of Eurasia than those of other mammalian taxa (Currant and Jacobi 2001). Fallow deer is a very common species in these deposits and is particularly well represented during the late Pleistocene (DiStefano 1995). Artiodactyls were especially important to late Pleistocene human economies (Guthrie 2000). From about 9,000 BP, red (*Cervus elaphus* Linnaeus, 1758), fallow and roe (*Capreolus capreolus* Linnaeus, 1758) deer were more common in deposits of this era than other cervids.

An accurate age determination of faunal skeletal material is essential to gain a greater understanding of many aspects of prehistoric economies (assessment of hunting, husbandry strategies and paleodemographic studies) (Amorosi 1989). Age estimation of mammals is usually by a combination of tooth eruption and development, attrition (crown height measurement and degree of wear), and counts of annuli in cementum (for example see Ohtaishi 1980; Stallibrass 1982; Brown and Chapman 1990, 1991; Carter 2001; Lubinski 2001; Hauer *et al*. 2002). However, cementum incremental analysis, which is destructive, is further contraindicated for archaeological specimens as they normally retain little organic matter to provide adequate histological differentiation (Klein *et al*. 1981). Furthermore, methods based on dental eruption and attrition of extant and archaeological specimens can only give an estimate of ontogenetic (developmental) age unless the estimate is calibrated by comparison with a reasonable large dataset of known (absolute or calendric) age.

Skeletochronology and range of skeletal growth variability have been documented and used as a reliable and effective, non-destructive method of age estimation in a wide variety of taxa such as reptiles (Caldwell 1996; Carter *et al*. 1998), amphibians (Trueb *et al*. 2000; Measey 2001), domestic mammals (Schlotthauer and Janes 1952; Silver 1963; Noddle 1974; Armitage 1982; Amorosi 1989; Davis 2000), and other wild mammals (Wight and Conway 1968; Morris 1971; Harris 1978; Chambers and Chambers 1982; Winkler 1996; Nakai 2001; Storå 2001). Bone structure changes with age by turnover, remodelling and growth, which alter the morphology and histology of the bone throughout an animal's life (Thomas *et al*. 2000). In mammalian long bone development, perichondral bone first appears followed by endochrondral ossification of the cartilage core in the

| Age Class | 0–12 | 13–24 | 25–36 | 37–48 | 49–60 | 61–72 | 73–84 | 85–96 | 97–108 | 108+ | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Male | 27 | 32 | 9 | 6 | 11 | 7 | 2 | 6 | 6 | 12 | 118 |
| Female | 29 | 21 | 10 | 6 | 1 | 2 | 2 | 0 | 1 | 20 | 92 |

*Fig. 1. Summarized age structure (months) and body numbers of sample material used in this study. Note: due to injury at death not all of the skeletal elements and parts thereof were available for suture observations; hence the differences in sample numbers between Fig. 1 and Figs 8 and 9.*

growing foetus within which centres of ossification develop (Carter *et al*. 1998). The longbone diaphysis (main shaft) is the first to appear. Growth, development and extension of the shaft proceed by proximal and distal replacement of cartilage by bone. A further centre of ossification, the epiphyseal centre, appears at both the proximal and distal ends of the diaphysis. The epiphyseal plate is a cartilage layer that grows to increase the length of a bone. The newly lengthened region is then stabilized and strengthened by replacement with bone (Opperman 2000). With increasing skeletal maturity, the epiphyseal plate becomes narrower and finally, when growth is complete, it is eliminated entirely, thereby uniting the bone as a single unit (Lewall and Cowan 1963). Thus unfused epiphyses are an indication of continuing growth and may serve as a guide to age (Morris 1972). The process of ossification is relatively constant for each epiphysis, thus once a skeleton has started to ossify, the age of an animal may be determined fairly accurately by noting the regions where epiphyseal fusion has occurred (Silver 1963). By noting fused and unfused epiphyses in the skeleton, as stated by O'Connor, the 'age can be bracketed: older than the earliest fusion time for the last fused epiphysis, but younger than the latest likely fusion time for the first epiphysis' (O'Connor 2000, 94).

This approach has been little used for cervid species (Todd and Todd 1938; Lewall and Cowan 1963; Knight 1966; Purdue 1983; Murray 1993) due to the lack of suitable reference material. In this paper, we present postcranial skeletal epiphyseal suture data for males and females of the highly sexually dimorphic European fallow deer and assess their uses in estimation of age at death.

## Materials and Methods

All fallow deer samples (male n=118, female n=92) were derived from an enclosed herd in Phoenix Park, Dublin, Ireland (53º22'N, 6º21'W). Fig. 1 summarises the age structure of the material used in this study. The sample of males ranged from 0 to 173 months (15 years), whereas the sample of females ranged from 0 to 273 months (22 years) of age.

Phoenix Park is located 2.4 km west of the centre of Dublin City and comprises of 709ha, of which approximately 80% is available to deer (Hayden *et al.* 1992). The vegetation of the park consists of large open areas of grassland with less than 25% of the land area covered by woodland, mainly deciduous (14%) with some areas of mixed wood (6%) and a small area of conifers (3%) (Jennings 2000). Phoenix Park is maintained and administered by the National Parks and Wildlife Service (NPWS), Department of the Environment, Heritage and Local Government.

Each year, since 1980, the Mammal Research Group (Zoology Department, National University of Ireland, Dublin) in conjunction with NPWS, tag the majority of the fawns with unique combination ear tags (Allflex), colour-coded (for year) and numbered. They can then be identified throughout their lifespan (Moore *et al.* 1995). Animals used in this study died directly or indirectly from road traffic accidents or from natural causes over a period of four years. Necropsy was performed between one to 14 hours after death.

### *General procedure for obtaining skeletal sets*

The following bone sets were removed where possible, from each carcass: scapula, humerus, radius, ulna, metacarpal, pelvis, femur, tibia and metatarsal. Depending on the injuries suffered at time of death by the animal, not all bones were recoverable. As much flesh as possible was removed and all bones were subjected to slow simmering with numerous water changes to remove remaining flesh and marrow. Every effort was made to retain all detached epiphyses in the skeletally immature animals but some were invariably lost. The bones were then cleaned in running hot water and allowed to dry slowly for between 36 to 48 hours in a well-ventilated room.

The effect of cleaning bones by burial was investigated by burying a small sample set (n=30) from a range of ages. These bones were interred, approximately two meters deep in well-drained soil for a duration of time between six to 10 months until all flesh and marrow had decomposed. The sutural pattern and epiphyseal detachment patterns were compared with homologous bones prepared using the simmering technique. No effect of method of preparation was detected thus the laboratory-based method was used.

| Bone | Code | Location |
|---|---|---|
| Scapula (SP) | SP1 | Tuberculum supraglenoidale |
| Humerus (H) | H1 | Caput humeri junction to diaphysis |
| | H2 | Tuberculum majus junction to diaphysis |
| | H3 | Junction between diaphysis and condylus humeri |
| | H4 | Junction between distal lateral and medial epipcondyles to condylus humeri |
| Ulna (U) | U1 | Junction between the olecranon and diaphysis |
| | U2 | Junction between the diaphysis and processes atyloideus ulnae |
| Radius (R) | R1 | Junction between caput radii and diaphysis |
| | R2 | Junction between diaphysis and trochlea radii |
| Metacarpal (Mc) | Mc1 | Junction between dorsal and palmar longitudinal grooves of large metacarpal |
| | Mc2 | Junction between the distal condyles and large metacarpal |
| | Mc3 | Junction between proximal carpal articular and large metacarpal |
| Pelvis (P) | P1 | Corpus ossis ischii-corpus ossis ilii junction |
| | P2 | Ramus caudalia ossis pubis-ramus ossis ischii |
| | P3 | Corpus ossis ilii-corpus ossis pubis |
| | P4 | Symphysis pubica |
| Femur (F) | F1 | Junction between diaphysis and distal condyle |
| | F2 | Proximal articular head (caput) junction to diaphysis |
| | F3 | Proximal trochanter major junction to diaphysis |
| | F4 | Proximal trochanter minor junction to diaphysis |
| Tibia (T) | T1 | Junction between proximal condylus and diaphysis |
| | T2 | Junction between tuberositas tibiae and diaphysis |
| | T3 | Junction between diaphysis and extremitas distalis |
| Metatarsal (Mt) | Mt1 | Junction between dorsal and palmar longitudinal grooves of chief metatarsal bone |
| | Mt2 | Junction between distal condyles and chief metatarsal bone |
| | Mt3 | Junction between proximal tarsal articular and chief metatarsal bone |
| Pelvic secondary ossifications | P5 | Crista iliac (cranial dorso-ventral surface) |
| | P6 | Ventral view of tuber ischiadium |

*Fig. 2. Postcranial epiphyseal sutures (n=26) and pelvic secondary ossifications (n=2).*

| Suture state | Description of state |
|---|---|
| **Unfused** (Uf) | Includes all detached epiphyses due to simmering/decomposition. Characterized by an obvious gap between epiphysis and diaphysis, if epiphysis present (attached only by cartilage). Epiphysis appears to be ill fitting and shrunken; diaphysis bone near epiphysis appears porous and pithy. *Age recorded*: the latest age that this state is observed in any given bone. |
| **Fusing** (Fg) | Incomplete fusion of epiphysis to diaphysis, a thin gap is visible. Bone has an incomplete 'knitted' appearance (like zipper teeth). No gap visible to the observer eye, but slight irregular ridge is visible. Observer should be able to follow suture line easily. *Age recorded*: the range between the earliest and latest ages at which this state is observed. |
| **Fused** (F) | Suture line is non-detectable, no open areas along fusion line. Bone is one complete unit. *Age recorded*: the likeliest age range during which the suture becomes fully fused to the diaphysis. |

*Fig. 3. Description of the epiphyseal suture states used in this study accompanied by Figs 4–7.*

### *Age and fusion states*

The sutural state was recorded for each of the individual bones from all sets. Age ranges of sutural fusion are used since bone fusion does not occur exactly at the same age in every individual. Fig. 2 describes the type and location of the epiphyseal sutures (n=26) and the pelvic secondary ossifications (n=2) used in this study, anatomical descriptions follow those of Nickel *et al.* (1986). During this work, we defined three stages of epiphyseal sutural state, unfused (Uf), fusing (Fg) and fused (F), as well as fusion of pelvic secondary bone ossifications/depositions in older adults (refer to Fig. 3 and Figs 4–7).

### *Estimated age at death of an individual animal*

Figs 8 (male) and 9 (female) can be applied to skeletal material to estimate age once epiphysis sutural data have been recorded. The estimated age range was determined by recording all sutures that were fused. The estimated age is then either less than or equal to this age, given in Figs 8 and 9. Then unfused epiphyses are recorded and the estimated age is either equal or greater than the age given. The age range at which the fusing epiphyses are observed can then be used to narrow down the estimated age range.

The accuracy and validity of the ageing method was tested using a blind sub sample (n=34) (see Fig. 10); this

*Fig. 4. Unfused epiphyseal suture state of F1. The distal condyle is attached via cartilage only. Newborn male fawn, absolute age 0 months.*

*Fig. 5. Fusing epiphyseal suture state of R1. Identity tag Y687 male, absolute age 4 months.*

*Fig. 6. Fusing epiphyseal suture state of F1. Identity tag G302 male, absolute age 39 months.*

*Fig. 7. Fused epiphyseal suture state of Mc2. For comparison, the metacarpal on the left displays the fused state of Mc2 (identity Y76 male absolute age 128mths), whereas the metacarpal on the right displays the unfused state of the suture (identity W409 male absolute age 11 months). The detached epiphysis is not shown.*

was randomly chosen by a colleague from the full set (n=210). This sample was aged using our method by one of the authors (R.C.).

## Results

The epiphyseal state patterns for each suture in male and female fallow deer and the order of complete fusion are given in Fig. 8 and 9 respectively. The results from these tables are summarised below for each age class.

### *Age 0–12 months (0–1 year)*

It was observed that the proximal epiphyses of both the metacarpal (Mc3) and metatarsal (Mt3) bones in males and females were fused entirely prior to birth. For 17 sutures in males and 16 in females from the total number of sutures (n=28), all specimens were unfused. In the case of eight of the sutures (H3, H4, R1, Mc1, P1, P2, P3 and Mt1), some specimens had begun the closure process and five (male) and four (female) sutures had progressed through all epiphyseal suture states and were fused by 12 months of age (males R1, Mc1, P1, P2, and Mt1; females R1, Mc1, P2 and Mt1).

| Epiphyseal Code | Sample size | Fused Age (mths) | Fusing Age (mths) | Unfused Age (mths) |
|---|---|---|---|---|
| Mc3 | 42 | prior to birth | | |
| Mt3 | 27 | prior to birth | | |
| Mt1 | 27 | 4–9 | 1–4 | 1 |
| R1 | 68 | 7–8 | 4–7 | 4 |
| P2 | 98 | 8–9 | 7–8 | 6 |
| Mc1 | 42 | n.a.–10.5 | n.a. | 1 |
| P1 | 100 | 10.5–12 | 9–10.5 | 9 |
| P3 | 99 | 10.5–13 | 9–10.5 | 8 |
| H3 | 81 | 14–15 | 7–14 | 4 |
| SP1 | 88 | 15–16 | 13–15 | 12 |
| F4 | 102 | 17–18.5 | 16–17 | 16 |
| H4 | 81 | 18–18 | 7–18 | 4 |
| T3 | 39 | 22–25 | 14–17 | 10.5 |
| F3 | 102 | 33–39 | 17–33 | 28 |
| U1 | 62 | 33–39 | 31.5–33 | 28 |
| Mc2 | 42 | n.a.–41 | n.a. | 15 |
| Mt2 | 27 | n.a.–41 | n.a. | 20 |
| T2 | 39 | 39–41 | 28–39 | 26 |
| H2 | 81 | 39–40.5 | 26–39 | 28 |
| R2 | 68 | 39–41 | 28–39 | 28 |
| F2 | 101 | 40.5–41.5 | 18.5–40.5 | 28 |
| U2 | 60 | 40–41.5 | 33–40.5 | 31.5 |
| T1 | 39 | 41.5–48 | 31.5–41.5 | 28 |
| F1 | 102 | 47–49 | 28.5–47 | 28 |
| P6* | 97 | 55–63 | 17–55 | 41.5 |
| H1 | 81 | 64–64.5 | 28–64 | 39 |
| P5* | 97 | 68–76 | 31.5–68 | 52 |
| P4 | 97 | 76–102 | 49–76 | 42 |

*Fig. 9. The epiphyseal suture states of male fallow deer and ages at which they occur in order of complete fusion with the sample number for each skeletal element. 'n.a.' denotes no data available.*

| Epiphyseal code | Sample size | Fused age (mths) | Fusing age (mths) | Unfused age (mths) |
|---|---|---|---|---|
| Mc3 | 31 | prior to birth | | |
| Mt3 | 23 | prior to birth | | |
| Mc1 | 31 | 4–4 | 1–4 | 1 |
| Mt1 | 23 | 4–9 | n.a.–6 | n.a. |
| R1 | 53 | 5–8 | 3–5 | 4 |
| P2 | 67 | 9–9 | 6–9 | 5 |
| P1 | 72 | 15–15 | 8.5–15 | 9 |
| P3 | 72 | 13–13 | 4–13 | 9 |
| H3 | 64 | 13–13 | 4–13 | 4 |
| H4 | 64 | 13–13 | 4–13 | 4 |
| T3 | 28 | 15–20 | 13–15 | 9 |
| SP1 | 68 | 17–20.5 | 13–17 | 9 |
| U1 | 50 | 20–n.a. | 20–n.a. | 20 |
| Mc2 | 31 | 20–20 | 17–20 | 15 |
| Mt2 | 23 | 20–20 | 17–20 | 15 |
| F4 | 80 | 20–20 | 13–20 | 13 |
| H2 | 64 | 38.5–45 | 20–38.5 | 20 |
| F3 | 80 | 38.5–39.5 | 20–38.5 | 20 |
| U2 | 37 | 38.5–45 | 20–38.5 | 27 |
| F1 | 80 | 39–40 | 27–39 | 20 |
| T2 | 28 | 39.5–75.5 | 27–39.5 | 20 |
| F2 | 80 | 40–44 | 20–40 | 20 |
| R2 | 53 | 45–45 | 20–45 | 20 |
| P6* | 72 | 45–54 | 27–45 | 40 |
| P5* | 72 | 54–66 | 20–54 | 45 |
| T1 | 28 | 75.5–121 | 27–75.5 | 20 |
| P4 | 70 | 76–110 | 44–76 | 45 |
| H1 | 64 | 108–110 | 34–108 | 37 |

*Fig. 9. The epiphyseal suture states of female fallow deer and ages at which they occur in order of complete fusion with the sample number for each skeletal element. 'n.a.' denotes no data available.*

### *Age 13–24 months (1–2 years)*

By two years of age, a subset of sutures, 43% of males (n=12) and 54% of females (n=15) had become fused. These were SP1, H3, H4, R1, Mc1, Mc3, P1, P2, P3, F4, Mt1 and Mt2 in males and females together with Mc2, T3 and Mt2 in females. From the remaining unfused sutures in females (n=13), seven of these, H2, R2, U1, U2, P5, F2 and F3 were fusing at 20 months of age. In contrast, four sutures from the remaining 16 sutures in males were fusing. These were P6, F2, F3 and T3.

### *Age class 25–36 months (2–3 years)*

Between the ages of two and three years, T3 was fused by 25 months of age in males. In some male specimens, U1 and F3 were fused by 33 months of age at the earliest. There were no newly fused epiphyses in the female specimens during this age class. No additional sutures in male specimens were fused; they were either unfused or fusing. Eight sutures in male specimens and five sutures in females had entered the fusing state. These were H1, H2, R2, U1, U2, P5, F1, T1, and T2 in males, and H1, P6, F1, T1 and T2 in females.

### *Age class 37–48 months (3–4 years)*

In males and females specimens, four additional sutures (H2, R2, U2 and F2) together with F1 and F3 in females and T1 and T2 in males had fused during this period. In some of the female specimens, two sutures (P6 and T2) were fused at their earliest during this period. Thus, by 48 months of age, 23 of the sutures of males and females (excluding U1 in females) from the total (n=28) were fused. These sutures common to both sexes were SP1, H2, H3, H4, R1, R2, U2, Mc1, Mc2, Mc3, P1, P2, P3, F2, F3, F4, T2, T3, Mt1, Mt2 and Mt3, male only: U1 and T1; female only: P6 and F1.

### *Age class 49–60 months (4–5 years)*

During this age class, in the single available female specimen (54 months old), both R2 and P6 were fused. The F1 suture in the male specimens was fused by 49 months of age. P6 was fused at its earliest during this period in males. Three remaining sutures in males (H1, P4 and P5) and three sutures in females (H1, P4 and T1) were fusing.

### *Age class 61–72 months (5–6 years)*

At this stage, between five and six years of age, the only additional epiphyseal sutures that were fused were H1 and P6 in males and P5 in females. In one of the male specimens, the P5 suture was fused.

### *Age classes 73–84 months (6–7 years)*

In males, the P5 suture was fused at 76 months of age at the latest, and T2 in females was fused at 75.5 months of age at the earliest. For both sexes, the P4 suture reached its earliest observed fused state at 76 months of age. In some individuals of either sex, the P4 suture had just achieved complete fusion by 76 months of age. In some females, T1 was fused by 76 months of age. But H1 in females was still in the fusing state.

### *Age class 85–96 months (7–8 years)*

No remaining sutures in either sex had attained the fused state. It was observed that the H1 suture in females was still in the state of fusing.

### *Age class 97–108+ months (8–9+ years)*

Between eight and nine years of age, the last remaining suture P4 had fused in all males at 102 months of age. In females, there were no further sutures displaying the fused state at this time. Between nine and 10 years, sutures H1 and P4 in females were fused by 110 months of age. The T1 suture in females fused at 121 months of age.

### *Accuracy of age estimation*

With reference to Fig. 10, results of the estimated age classes can be compared to those of the known ages of males and females. For female fallow deer, 10 individuals were correctly assigned to their absolute age class; these were individuals aged up to six years of age. The remaining eight individuals that were aged nine years and older were estimated older than seven years of age. In males, 12 of the 13 individuals of known age were assigned to their correct age class, aged up to six years of age. A further three males who were aged eight years and older, were estimated to be older than seven years of age.

### *Age at death: worked example*

We illustrate our age estimation method using the epiphyseal suture states applied to B203 a male whose absolute age at death was 65 months. Postcranial epiphyseal sutures in the pelvis, femur, tibia, scapula, humerus, ulna and radius were recorded and are presented in Fig. 11. The sutures of the humerus, ulna, radius, scapula and tibia were all fused but both P4 and P5 exhibited the fusing state. Reference to Fig. 8 reveals that as the majority of these reach the fused state at a relatively early age, we can assume that the animal is older than two years of age. P4 (*symphysis pubica*) is fusing indicating that the animal is at least 76 months of age but may be as young as 49 months. However, another late fusing epiphyseal suture is H1 (*caput humeri*). B203 exhibits the fused state of this suture, which occurs between 64–64.5 months. The animal is approximately

| I.D. tag sex | Bone material, code and number | Absolute age (mths) | Absolute age class (years) | Estimated age (mths) | Estimated age class (years) |
|---|---|---|---|---|---|
| Y691 f | P,F,Sp,H (4) | 7 | 0–1 | 9–13 | 0–1 * |
| B540 f | P,T,Sp,H,U,R (6) | 9 | 0–1 | 9–13 | 0–1 * |
| W535 f | P,F,Sp,H,U,R (6) | 13 | 1–2 | 9–17 | 1–2 * |
| W403 f | P,F,Sp,H,R (5) | 13 | 1–2 | 13–17 | 1–2 * |
| W424 f | P,F,Sp,H,U,R (6) | 27 | 2–3 | 27–38.5 | 2–3 * |
| G346 f | P,F,Sp,H,U,R (6) | 36 | 3–4 | 39–45 | 3–4 * |
| G337 f | P,F,T,Sp,H,U,R (7) | 38.5 | 3–4 | 38.5–40 | 3–4 * |
| P820 f | P,F,Sp,H,U,R (6) | 45 | 3–4 | 40–45 | 3–4 * |
| B273 f | P,F,Sp,H (4) | 54 | 4–5 | 54–76 | 4–5 * |
| Y360 f | P,F,Sp,H (4) | 66 | 5–6 | 66–76 | 5–6 * |
| O209 f | P,F (2) | 114.5 | 9–10 | 76–110+ | 6–7 |
| B142 f | P,F,Sp,H,U,R (6) | 129.5 | 10–11 | 108–110+ | 9–10 |
| Y207 f | P,F,T (3) | 135 | 11–12 | 76–121+ | 6–7 |
| O111 f | P,F,Sp,H (4) | 149.5 | 12–13 | 108–110+ | 9–10 |
| O232 f | P,F,T,Sp,HU,R (7) | 159 | 13–14 | 108–121+ | 9–10 |
| G47 f | P,F,Sp,H,U,R (6) | 185 | 15–16 | 76–110+ | 6–7 |
| G40 f | P,F,T,Sp,H,U,R (7) | 188.5 | 15–16 | 110–121+ | 9–10 |
| O106 f | P,F (2) | 273 | 22–23 | 76–110+ | 6–7 |
| Y698 m | P,F,Sp,H (4) | 7 | 0–1 | 7–9 | 0–1 * |
| Y631 m | P,F,T,Sp,H,U,R (7) | 9 | 0–1 | 7–9 | 0–1 * |
| W436 m | P,F,Sp,H (4) | 16 | 1–2 | 15–18 | 1–2 * |
| W412 m | P,F,Sp,H (4) | 17 | 1–2 | 16–18 | 1–2 * |
| W418 m | P,Sp,H (3) | 18 | 1–2 | 13–18 | 1–2 * |
| W430 m | P,F,T,Sp,H,U,R (7) | 26 | 2–3 | 22–25 | 2–3 * |
| W540 m | P,F,T,Sp,H,R (6) | 28 | 2–3 | 22–25 | 2–3 * |
| G302 m | P,F,T,Sp,H,U,R (7) | 39 | 3–4 | 39–41 | 3–4 * |
| P868 m | P,F,Sp,H,U,R (6) | 50 | 4–5 | 40.5–64.5 | 4–5 * |
| Y322 m | P,F (2) | 54 | 4–5 | 68–76 | 5–6 |
| Y220 m | P,F (2) | 64 | 5–6 | 68–76 | 5–6 * |
| B203 m | P,F,T,Sp,H,U,R (7) | 65 | 5–6 | 64.5–76 | 5–6 * |
| Y357 m | P,F,Sp,H,U,R (6) | 68 | 5–6 | 64–76 | 5–6 * |
| W209 m | P,F,Sp,H,U,R (6) | 100 | 8–9 | 76–102+ | 6–7 |
| O176 m | P,F,Sp (3) | 130 | 10–11 | 76–102+ | 6–7 |
| B108 m | P,F,Sp,H,U,R (6) | 136 | 11–12 | 76–102+ | 6–7 |

*Fig. 10. Results from the blind sub-sample (n=34) to test the accuracy of our method. The identity (I.D.), sex (m, f) and absolute age (months) of the bone sets were uncovered after the initial exercise of recording the epiphyseal fusion states (Fig. 2) and estimating the age range (months) of the bone sets using Figs 8 and 9. * denotes those individuals whose ages were estimated and correctly assigned to their absolute age class.*

65 months of age. In older adults the secondary ossifications of the pelvis are quite important in estimation of age. The P5 secondary ossification suture is exhibiting the fusing state, with reference to Fig. 8, B203 is at least 68 months of age, but may be as young as 31.5 months. The other pelvic secondary ossification is P6 (*tuber ischiadicum*), which is fused between the age range of 55–63 months. Hence the animal is estimated to be at least 76 months old, but may be as young as 68 months.

## Discussion

In our study we found that skeletal elements can be used with confidence to estimate the age of fallow deer up to eight years of age. The ontogeny of sexual size dimorphism of this cervid permits the confounding effect of sexual differences in skeletal development to be accounted for. The method therefore permits the assignation of an individual to one of a number of key life stages of interest to archaeologists and zoologists.

Fallow deer are highly sexually dimorphic. Males weigh two and a half times that of females (Moore *et al*. 1995; McElligott *et al*. 2001). The sexual dimorphism in the postcranial skeleton is due to the higher rate and longer duration of the growth phase of males than that of females. This difference of bone growth (e.g. length and diameter) between male and female fallow deer occurs after approximately 10 months of age. Prior to this, skeletons can be sexed based on pelvic and cranial features (Carden and Hayden, unpublished data). Additionally, Nugent (1989) demonstrated that fallow deer more than two years of age could be sexed reliably from jawbone measurements. This is important when epiphyseal fusion patterns differ between the sexes. For a species that does not exhibit sexual size dimorphism, it will be problematic to distinguish skeletal elements between males and females. The number of life stages and age classes that can be distinguished depends on the longevity and sex-specific mortality of a species. In this study, we have shown that males and females can be aged up to eight years. What are the implications of being unable to discriminate

| Epiphyseal suture | Estimated epiphyseal state | Estimated age (months) |
|---|---|---|
| R1 | F | 7–8+ |
| P2 | F | 8–9+ |
| P1 | F | 10.5–12+ |
| P3 | F | 10.5–13+ |
| H3 | F | 14–15+ |
| SP1 | F | 15–16+ |
| H4 | F | 18–18+ |
| F4 | F | 17–18.5+ |
| T3 | F | 22–25+ |
| P5 | Fg | 31.5–68 |
| F3 | F | 33–39+ |
| U1 | F | 33–39+ |
| R2 | F | 39–41+ |
| T2 | F | 39–41+ |
| H2 | F | 39–40.5+ |
| F2 | F | 40.5–41.5+ |
| U2 | F | 40–41.5+ |
| T1 | F | 41.5–48+ |
| P4 | Fg | 49–76 |
| F1 | F | 47–49+ |
| P6 | F | 55–63+ |
| H1 | Fg | 28–64 |

*Fig. 11. Results of the worked example to estimate the age of an individual animal. Using the postcranial epiphyseal sutural states of a male fallow deer, B203, the estimated age of the epiphyseal stages is based on Fig. 8. B203 absolute age is 65 months (5–6 yr age class). Estimated age (68–76 mths): B203 is at least 76 mths of age but may be as young as 68 mths (5–6 yr estimated age class).*

between animals older than eight years of age? Examination of the age distribution of a fallow deer population reveals that the residual older animals only represent approximately 20% of females and 5% of males in the population. This is due to the higher age-specific mortality at all ages of males (Hayden *et al*. 1992).

We found that the order of epiphyseal fusion pattern in fallow deer is similar to that of white-tailed deer and black-tailed deer (Lewall and Cowan 1963; Purdue 1983). A subset of six sutures (H3, H4, R1, P1, P2 and P3) were fused at about two years of age in both sexes in these species and in fallow deer. However, in animals older than two years of age, the sutures were fused at a younger age for white tailed deer and black tailed deer when compared with fallow deer. This may be a consequence of the contrasting life-history strategies of telemetacarpalian (eg. white-tailed deer) and plesiometacarpalian (eg. fallow deer) species (Harrington 1985). Purdue's (1983) study of white-tailed deer found that there was an overall trend of the female elements fusing prior to those of the males, and the sexual differences were most pronounced in late fusing epiphyses. In our study, we found that from 10 late-fusing sutures (H1, H2, R2, P4, P5, P6, F1, F2, T1 and T2) in both sexes aged 40 months and older, three of these were fused in males prior to females. These were H1, R2 and T1. Only three sutures P5, P6 and F2 were fused in females prior to males and four sutures common to both (H2, P4, F2 and T2) were fused at relatively the same age.

A method of age estimation ideally should be simple to use, unambiguous and non-destructive of the specimens and appropriate to the study material. In archaeofaunal assemblages, epiphyses (fusing or fused to the diaphysis) are often the most numerous age-related features observable, and are far more common than complete tooth rows (Amorosi 1989). Skeletal sets examined in this study contain bones that are commonly found whole or in part in archaeological deposits. These are the distal portions of the scapula, humerus, radius and tibia; proximal portions of the radius, ulna, femur and tibia; the acetabulum of the pelvis, together with whole bones such as the radius and tibia (von den Driesch 1976). Epiphyseal fusion and tooth eruption sequences are well known for domestic animals, but vary among breeds, as well as among male, female and castrated animals, but data of this kind are scarce for most wild mammals (Reitz and Wing 1999). The sequence of epiphyseal fusion in an individual is regular, but the age at which fusion occurs is variable (Chaplin 1971).

Like all age-estimation methods, there are certain limiting factors associated with epiphyseal sutural fusion and the estimated age of death, methods which usually assume that the animals were healthy. Factors such as the nutritional environment can determine the skeletal size of an animal (Nugent and Frampton 1994). Skeletal development in terms of epiphyseal fusion can be delayed by disease, trauma, chronic malnourishment and castration of males (Noddle 1974; O'Connor 2000). Malnutrition of an animal affects body growth and skeletal development and consequently the epiphyseal pattern, and this is reflected in a delayed epiphyseal fusion development. Furthermore, disturbances in body growth can also affect fusion, causing premature fusing of epiphyses (Storå 2001). In addition, when comparing modern breeds/species to ancient ones, it does not always follow that their growth patterns will be the same.

Epiphyseal fusion can be used in conjunction with other ageing methods, such as tooth eruption, to estimate age only to skeletal maturity. Adult dentition is completed long before complete skeletal maturity and thus epiphyseal fusion can be used as a crosscheck for data derived from dental eruption and attrition (O'Connor 2000). For example in fallow deer, the last molar, M3, of the lower mandible comes into wear between 28 to 35 months of age (Moore *et al*. 1995). Beyond this, age estimates based on wear require a reference collection of animals of known age from that locality to control for dietary wear or tooth attrition. Epiphyseal fusion rates are less sensitive to

these affects. White-tailed deer skeletal samples from a diversity of habitats and, therefore, a high diversity of forage did not exhibit any correlation between geographic location and epiphyseal fusion (Purdue 1983). Tooth eruption and attrition has had a long tradition as the method for mammalian age estimation (for example Brown and Chapman 1990; Lubinski 2001), however, mandibles may be affected through human intervention such as tool making. Bones or bone fragments bearing epiphyses are commonly found in larger numbers and, therefore, may permit meaningful age-distributions. This may allow a better understanding of hunting strategies as has been shown for reindeer (*Rangifer tarandus*) in the Late Glacial site of Stellmoor, Northern Germany (Weinstock, 2000) and the exploitation of seals (*Phoca* sp.) by Neolithic inhabitants of the Baltic (Storå, 2002).

Our study highlights the importance of known aged mammals in the study of age estimation using epiphyseal suture fusion patterns. Our method has application in the fields of zooarchaeology and wildlife management biology, where faunal skeletal elements are found. In addition, it should be noted that a complete skeleton is not required to accurately estimate the age of an individual animal, and epiphyseal sutural fusion can be usefully employed in conjunction with other methods of estimating age of faunal skeletal material.

*Acknowledgements*

We thank Mr. John McCullen, Superintendent of Phoenix Park, NPWS and the Wildlife Rangers and staff of Phoenix Park for their assistance and support, in particular, Mr. Don Doran (Deerkeeper). We thank M. Gammell for the random subsample. We are also grateful to fellow members of the M.R.G. and others for assistance in the field, in particular: C. Carlin, C. Collins, C. Fitzpatrick, M. Gammell, H. Harty, D. Jennings, F. Moran, D. O'Brien, R. O'Brien, S. Rooney and D. Walshe. R. Carden gratefully acknowledges the assistance of Nessa O'Connor (digital photography). We are grateful to D. Jennings, D. Carden, M. Gammell and two anonymous reviewers for comments on earlier versions of this manuscript. This paper was originally presented as part of the 'Ageing and Sexing session' organised by Deborah Ruscillo at the 9th conference of ICAZ meetings at the University of Durham, England 23rd–28th August 2002. R. Carden gratefully acknowledges funding obtained from the Institute for Aegean Prehistory (INSTAP) and Zoology Department, N.U.I. Dublin to attend and participate in this conference. We remember Mrs. Nuala Doran, ar dheis Dé go raibh sí.

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# 16. Size Variability in Roman Period Horses from Hungary

*K. Lyublyanovics*

*The discovery of three complete horse skeletons near the 2nd–3rd century AD Roman auxiliary fort of Albertfalva (modern Budapest, in the Roman province of Pannonia) provided an opportunity for studying three possible sources of size variability in the long bones of this species: age, sex and phenotype. A comparison with other Roman Period horse finds showed that the stature of Albertfalva animals was large with withers height estimated at 150–160 cm, a respectable stature even by modern standards. A source of phenotypic size variability may have been the impact of "indigenous" Celtic stocks (smaller animals that survived Roman occupation in the area), as well as a result of the import of large, "western" type horses from Italy or other provinces in the Roman Empire. A proper evaluation of size, however, is not possible without attempting to consider the animal's ontogeny and sexual dimorphism, the latter being rather poorly expressed in the morphometry of horse bones.*

## Introduction

During the excavations at Albertfalva near Budapest in 2001, Roman Period animal remains were recovered from an area just outside the *vicus* surrounding the auxiliary fort (Szirmai 2000). Three complete horse skeletons were discovered by the archaeologists on the eastern side of the excavation area; some Roman ceramic sherds were also recovered from the pits where these horses were buried. The remains are relatively poorly preserved: the skulls are completely fragmented, so neither the measurement nor the definition of phenotype of the skulls is possible. Beside the horses, a cattle tibia and a sheep astragalus also were discovered.

The animal remains are now housed in the collections of the Aquincum Museum, Budapest. The terminology used in this paper and the methodology of the measurements follows von den Driesch (1976), the only modification being the measurement of smallest (diaphyseal) depth on long bones in addition to the smallest diameter, i.e. smallest breadth of the diaphysis. (The corresponding abbreviations are: SB = smallest breadth of the diaphysis, SD = smallest depth of the diaphysis). Estimations of withers height were made using Kiesewalter's method (1888).

## Description of the Remains

The first horse skeleton, Horse 1, was discovered in over 420 different fragments, although the skeleton is almost complete (only some of the caudal vertebrae are missing). Of the skull, only some fragments of the *os frontale*, the *os lacrimale*, the *os zygomaticum*, the *condylus occipitalis*, the *os petrosum* and the maxilla could be identified. On the basis of the teeth ($I^{1-3}$, C, $P^{2-4}$, $M^{1-3}$), the animal died at five years of age; the well-developed canines show that it was a stallion. The long bones are wide and well grown; the metatarsal bones are 19% longer than the metacarpals, their slenderness index (Brauner 1916) is 11.7. The phalanges reflect a strong pastern. The withers height estimated from the long bones is 147.3 cm, a "normal" size for Roman Period military horses. The corpus of the last two lumbar vertebrae are fused together, without exostosis (Fig. 1). This degree of fusion is not pathological in heavy horse types, although it is quite rare in such young specimens – possibly a combined result of ageing and riding.

The bones of the second horse, Horse 2, were found in 248 fragments. This 8 years old stallion seems to have been the largest of the three individuals discovered (161.7 cm estimated withers height). Its femora are long (436

*Fig. 1. The two last lumbar vertebrae of Horse 1 (top) and Horse 2 (bottom).*

and 433 mm). The corpus of the last two of the lumbar vertebrae are fused together without exostosis (Fig. 1). Also the *os tarsale primum*, *secundum et tertium* are fused into a single bone. Three of the molars are missing and only the *os incisivum* and some mandibular fragments are preserved from the skull. The canines are large and well-developed. The metatarsal bones are 18% longer than the metacarpals; their slenderness index is 12.26. The limbs are remarkably elongated; they were slender probably also in relation to the body as a whole. The right humerus and radius, as well as the femora on both sides, are incomplete although the greatest length of the bone can be measured.

The skeleton of the third individual, Horse 3, is the least well-preserved. Of the bones of the hind leg, only the femora were found. No canines were recovered while the pelvis is too fragmented to be of aid in identifying the sex of the animal. Only some of the molars and premolars were found and the skull is totally fragmented. The incisor teeth are also missing, so we can only identify that the horse was an adult specimen. The long bones discovered, especially the radii, are very long. The withers height was estimated as 158.6 cm but this calculation is based only on the femora and the long bones of the front legs. No pathological phenomena were discovered on the bones.

Details on the estimations of withers heights for all three specimens are summarized in Fig. 2.

***Comparison and Comments***

These horses offered a good opportunity to examine variability in Roman Period military horses in the province of Pannonia Inferior since these animals were buried close to each other in the same field and, presumably, within a short time period relative to each other. Identifying the sex of these animals is an interesting problem. The tall estimated withers height is not extreme for the species but unusually tall for Roman horses. This may indicate that these horses were castrated, even though coeval authors (Plinius, Columella, Varro) note that the Roman military preferred stallions to geldings. Another problem is the phenotype of these animals. There is extreme variability within the military horse type, and these animals are larger and stronger in skeletal structure than most of the horses used by the Romans at this time. We can analyze and compare the measurements with other Roman Period horse remains or with modern horses. The results may also be compared with contemporary artistic renderings of horses.

The horses under discussion probably belonged to the large Roman military horse type (Bökönyi 1974) with a withers height of 145–155 cm. Osteological remains of such animals have been discovered everywhere in the former area of the Roman Empire, along with the small local horses of the region. They represented a large and powerful type but were not identical with present-day heavy, "cold blooded" horses. The average withers height of the Roman horses was estimated as 142.9 cm by Bökönyi (1974). The same value for 144 horses from the Roman town of Tác–Gorsium was 139.07 cm (Bökönyi 1984, 61).

***Phenotypic differences***

The horse population of Europe became mixed during the Roman Period, to a great extent because military horses from Africa and Asia that could be transported to any province of the Empire. The "Roman military horse type" was, above all, a mixture of animals from Scythia, Persia and Hispania, and even though contemporary authors called them a "breed", it was not a separate breed, but should rather be considered a type. Some authors distinguished different horses for soldiers and for officers within this type, others considered it to be a uniform type (Hilzheimer 1924). Remains of such horses have been discovered in many places in the former province of Pannonia Inferior (Tác, Győr, Albertfalva). Some eastern troops were sent to Pannonia during the 2nd century AD. This makes it very likely that Syrian and Thracian horses were taken to this area as well. They presumably contributed some southern characteristics to the horse population. Most of the horses brought here belonged, however, to the "western" type. A statuette discovered at Tarhos-Vincesziget (Hungarian National Museum, Budapest) is a nice representation of this type. Another

| **Horse 1(dental age: 5 years)** | *Left* | | *Right* | |
|---|---|---|---|---|
| *Bone* | *GL* | *Withers height* | *GL* | *Withers height* |
| humerus | 303.5 | 151.75 | 311.1 | 155.55 |
| radius | 341.0 | 147.99 | 333.0 | 144.52 |
| metacarpus | 228.1 | 143.00 | 228.1 | 143.0 |
| phalanx proximalis | 89.1 | – | 85.0 | – |
| phalanx media | 49.9 | – | 49.0 | – |
| femur | 407.8 | 143.14 | 402.2 | 141.18 |
| tibia | 361.1 | 157.44 | 359.6 | 156.79 |
| metatarsus | 272.0 | 142.31 | 269.8 | 141.14 |
| astragalus | 62.3 | – | 57.9 | – |
| calcaneus | 114.0 | – | 112.3 | – |
| phalanx proximalis | 90.1 | – | 90.1 | – |
| phalanx media | 47.0 | – | – | – |
| **Horse 2 (dental age: 8 years)** | | | | |
| humerus | 335.8 | 167.90 | 335.7 | 167.85 |
| radius | 374.0 | 162.31 | 375.0 | 162.75 |
| metacarpus | 251.8 | 158.19 | 251.4 | 157.94 |
| phalanx proximalis | 89.0 | – | 89.2 | – |
| phalanx media | 50.3 | – | 49.2 | – |
| femur | 436.1 | 153.07 | 433.1 | 152.02 |
| tibia | 401.0 | 174.83 | 397.2 | 173.18 |
| metatarsus | 296.1 | 155.16 | 296.9 | 155.58 |
| astragalus | 70.1 | – | 72.0 | – |
| calcaneus | 122.2 | – | 122.1 | – |
| phalanx proximalis | 92.1 | – | 93.1 | – |
| phalanx media | 48.3 | – | 48.9 | – |
| **Horse 3 (adult)** | | | | |
| humerus | – | – | – | – |
| radius | 383.1 | 166.26 | 381.3 | 165.48 |
| metacarpus | 249.8 | 156.61 | 251.3 | 157.87 |
| phalanx proximalis | – | – | 93.1 | – |
| phalanx media | 51.9 | – | – | – |
| femur | – | – | 418.2 | 146.79 |

*Fig. 2. The greatest length of bones (GL) and estimated withers heights of the horses. All measurements in mm.*

parallel representation is the equestrian statue of the Roman Emperor Marcus Aurelius in Rome. The type was not homogeneous. The animals found at Albertfalva also seem to show characteristics of different phenotypes in the skeletal structure of their extremities. This may be viewed within the context of other horse types in Fig. 3. Other types in this table include the greatest lengths of long bones from 6–8th century Avar Period burials (see Bartosiewicz, this volume), since these horses are best represented by complete skeletons in Hungarian archaeozoology. Metapodial lengths of general modern horses, as well as extremely large heavy, cold-blooded horses and small ponies were also included for comparison.

The long bones of the newly discovered Albertfalva animals are longer and wider than the average lengths and widths of bones from coeval Roman military horses elsewhere. The metapodials of Avar horses, used by "nomadic" light cavalry (judged from the discovery of most such stallions and geldings in warriors' graves) are only slightly smaller but more uniform (S.D. values for metapodials) than the metacarpal and metatarsal bones of Roman military horses. The Albertfalva individuals, however, far exceed both averages. The metatarsal length of Horse 2 actually reaches the lower size range of modern-day heavy (cold-blooded) horses. Modern Asiatic wild horses (*Equus przewalskii*) and ponies in Fig. 3 illustrate equid size variability, i.e. how small horse metapodial lengths may be.

### *Effects of age*

Of the long bones, robust metapodials tend to be the best preserved. Conclusions in the literature, therefore, have been primarily based on these bones. However, various bones of a complete skeleton may yield different estimates. It is at this point that the age of the animals become of decisive importance. Metapodial growth ends early so that age does not influence metapodial lengths in adult specimens. This is clearly illustrated by the greater S. D. values of greatest lengths of more proximally located long bones in Avar horses (Fig. 3).

Transversal measurements, on the other hand may further increase, to compensate for the increasing live weight of animals. In addition, other factors (locomotor problems or failures in the limbs), however, may effect metapodial proportions. According to Guoth (1959), the loading on metatarsal bones has a more frontal than sagittal direction in heavy horses. Consequently, the diaphysis of the metatarsus in such animals is rather wide than deep. In thoroughbreds and trotters, the depths of metatarsals are larger than their widths, or the two are equal. Both Horses 1 and 2 from Albertfalva belong to the group of heavy horses on the basis of the diaphyseal width to depth proportions of the metatarsal bones. (The metatarsal bones of Horse 3 are missing). In Horse 2, the difference between metatarsal depth and width is almost 7 mm, greater than Horse 1. This difference supports the theory that the animals were similar to modern-day heavy horse types in their skeletal structure. Horse 2, however, also had a respectable stature and its limbs were longer in relation to the body.

According to the greatest length – smallest breadth proportions (slenderness indices) of the metatarsal bones, Horse 1 fits within the group of coeval military horses while the metatarsals of Horse 2 are larger than the average but also much more slender (the slenderness index is 12.26; Fig. 4*).* This slenderness sets them apart from modern heavy horses, whose metatarsal lengths Horse 2 has reached. Metatarsal proportions of Horse 2, however, nearly reach those of English thoroughbreds but are smaller. The slenderness index of metatarsus in Horse 1 seems to be closer to those of other Roman Period horses or recent half-bred types. Both horses have larger metatarsals than wild horses.

The aforementioned differences are less marked between the metacarpal bones. All three Albertfalva horses fit within the group of coeval Roman military horses, and all measurements are larger than those of

| Horse type | | humerus | radius | metacarpus | femur | tibia | metatarsus |
|---|---|---|---|---|---|---|---|
| Horse 1 | | 307.3 | 337.0 | 228.1 | 405.0 | 360.4 | 270.9 |
| Horse 2 | | 335.8 | – | 251.6 | 434.6 | 399.1 | 296.5 |
| Horse 3 | | – | 382.2 | 250.6 | 418.2 | – | – |
| Roman Period horses[1] | mean= | – | 322.6 | 228.1 | – | 374.0 | 266.3 |
| | min= | | | 206.5 | | | 238.5 |
| | max= | | | 262.5 | | | 296.0 |
| | S.D.= | | | 10.7 | | | 14.2 |
| | n= | | 3 | 77 | | 2 | 44 |
| Avar Period horses[1] | mean= | 286.3 | 334.6 | 222.9 | 391.8 | 348.5 | 266.2 |
| | min= | 261.0 | 312.0 | 206.0 | 367.0 | 322.0 | 250.0 |
| | max= | 311.0 | 358.0 | 240.0 | 413.0 | 374.0 | 282.0 |
| | S.D.= | 9.4 | 11.9 | 8.1 | 12.7 | 11.5 | 8.5 |
| | n= | 37 | 40 | 52 | 32 | 35 | 56 |
| *Equus przewalskii* (modern)[2] | mean= | – | – | 214.8 | – | – | 255.9 |
| | min= | | | 197.0 | | | 234.0 |
| | max= | | | 231.0 | | | 272.0 |
| | S.D.= | | | 6.3 | | | 7.4 |
| | n= | | | 31 | | | 32 |
| Heavy (cold-blooded) horses (modern)[2] | mean= | – | – | 268.2 | – | – | 307.2 |
| | min= | | | 253.0 | | | 289.0 |
| | max= | | | 288.0 | | | 324.0 |
| | S.D.= | | | 15.6 | | | 15.7 |
| | n= | | | 5 | | | 5 |
| Ponies (modern)[2] | mean= | – | – | 164.5 | – | – | 203.0 |
| | min= | | | 131.0 | | | 161.0 |
| | max= | | | 187.0 | | | 230.0 |
| | S.D.= | | | 25.1 | | | 30.7 |
| | n= | | | 4 | | | 4 |

*Fig. 3. Greatest length (mm) of the long bones from the Albertfalva horses and from other types of horse. S. D. stands for standard deviation. [1] Bökönyi 1974, 1984; [2] Eisenmann and Beckouche 1986.*

*Equus przewalskii* and smaller than those of modern heavy ("cold-blooded") horses. The metacarpal bones of Horse 2 and 3 are nearly as long as the metacarpals of the smallest modern heavy horses available for study, but they are 5 mm narrower. The metacarpus of Horse 1 is of average length, but wider than in most Roman Period horses.

While their metacarpal bones are not much longer than those of other Roman Period horses, the withers height of Horses 2 and 3 is much larger since all of their long bones are longer than average. Albertfalva horses stand out because all long bones were used in the estimation. In other Roman horses which have been studied, estimations are based on early fusing metapodia. In Fig. 5, variation along this axis may be the result of different combinations of extremity elements, including late fusing stylopodium bones contributing to each data point. The effect of age, in this case, is expressed in the different degrees of epiphyseal fusion that varies with age among the long bones.

When radius measurements are compared to those of other horse types (Fig. 6), the lengths of Albertfalva horse radii reach the values measured on heavy horses and racehorses (English thoroughbred). Their widths, however, are somewhat smaller. The bone proportions of Horses 2 and 3 are similar to those of the English thoroughbred. The radii of Horse 1 are shorter but the width and the depth almost attain the values characteristic of heavy horses and racehorses. The proportions of this bone suggest that the animal belonged to another phenotype. The length and the smallest depth of the radius in Horses 2 and 3 compares to that of trotters and English thoroughbreds, although the smallest width of these bones is larger. In Horse 1, this bone is much shorter but the width and the depth nearly reach the values measured on trotters and thoroughbreds.

The analysis of long bones makes it clear that the three animals represent two different kinds of structure within one horse type. Horse 1 seems to be a smaller example of the type, with wider limbs in relation to the body; it can be said that this animal is a typical representative of the Roman military horse. The other two horses were larger, with long and slender limbs (metatarsal measurements even reflecting the proportions of heavy horses).

### *Effects of sex*

We can expect that all three horses from Albertfalva were stallions or geldings. The well-developed canines of Horses 1 and 2 demonstrate that they were not mares. The size of Horse 3 suggests that this specimen was

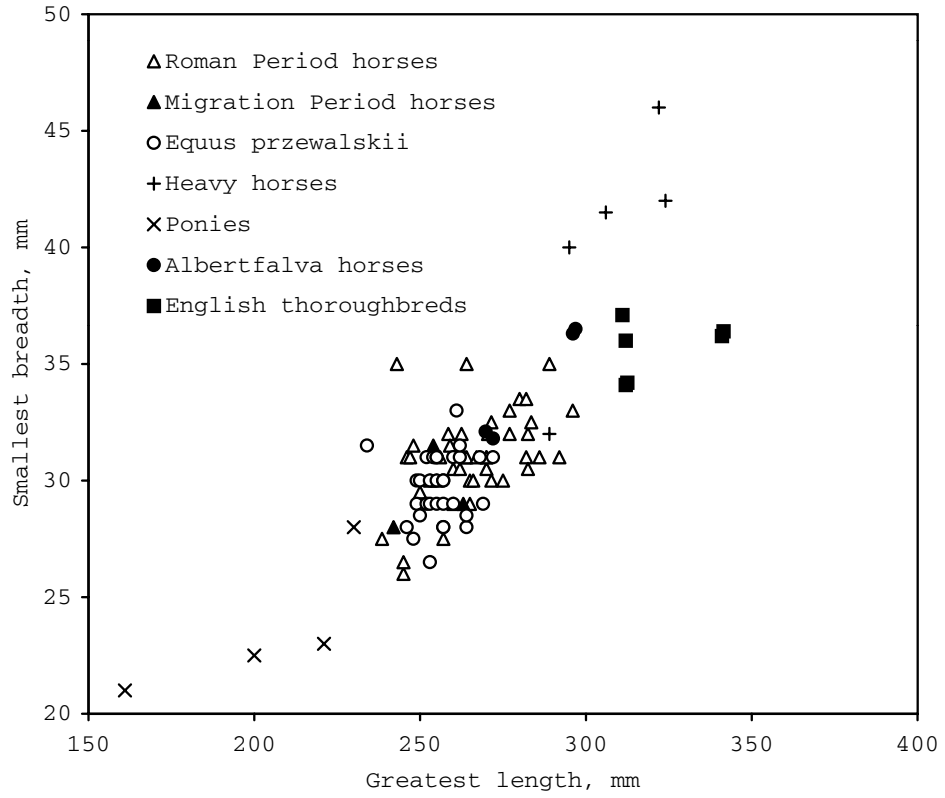


*Fig. 4. Proportion of the metatarsal bone.*

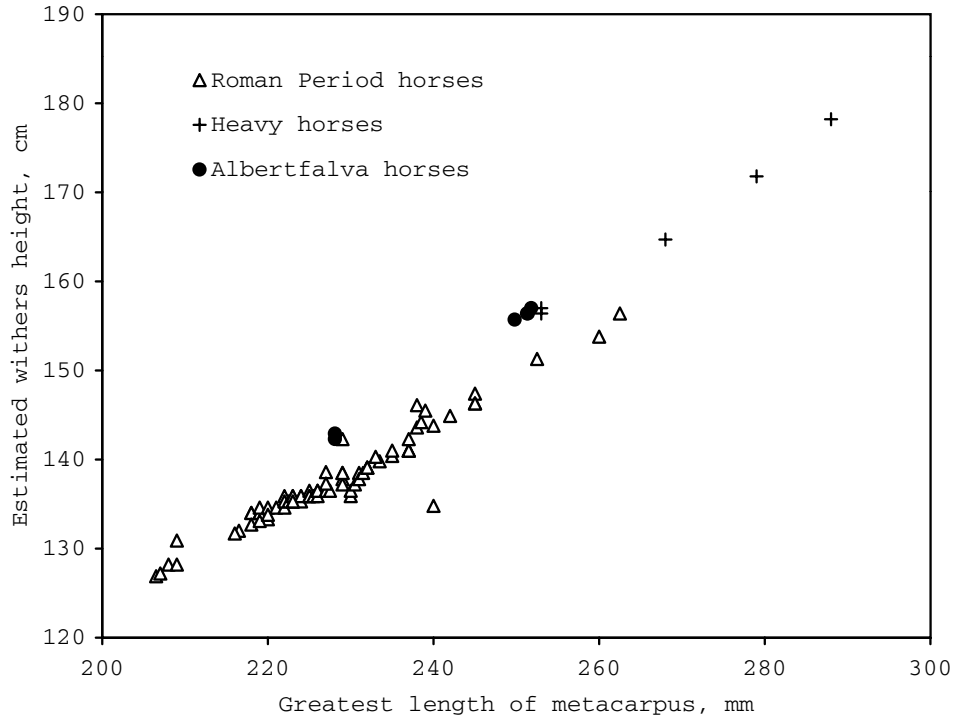


*Fig. 5. The greatest length of metacarpal bones in relation to withers height estimated from various long bones.*

| **Horse type** (Fehér and Nagy 1959) | *Greatest length* | *Proximal* | | *Smallest* | | *Distal* | |
|---|---|---|---|---|---|---|---|
| | | *width* | *depth* | *width* | *depth* | *width* | *depth* |
| Heavy "cold-blooded" horses* | 363.7 | 99.8 | 62.0 | 56.0 | 41.0 | 99.8 | 65.0 |
| "Cold-blooded" horses* | 362.0 | 92.6 | 62.0 | 42.0 | 30.0 | 85.8 | 53.0 |
| Trotters* | 384.4 | 98.8 | 48.0 | 45.0 | 32.0 | 93.0 | 49.0 |
| Racehorses* | 381.0 | 92.9 | 52.0 | 40.0 | 32.0 | 84.5 | 50.0 |
| Albertfalva | | | | | | | |
| Horse 1 | 337.0 | 87.9 | 53.2 | 41.0 | 30.1 | 79.6 | 46.7 |
| Horse 2 | 382.2 | 87.2 | 67.0 | 43.2 | 32.9 | 83.3 | 50.4 |
| Horse 3 | 382.2 | 88.4 | 52.8 | 40.4 | 31.5 | 80.2 | 48.3 |

*Fig. 6. Radius measurements of the Albertfalva horses and other horse types. *Sample sizes used in these calculations are unfortunately unknown.*

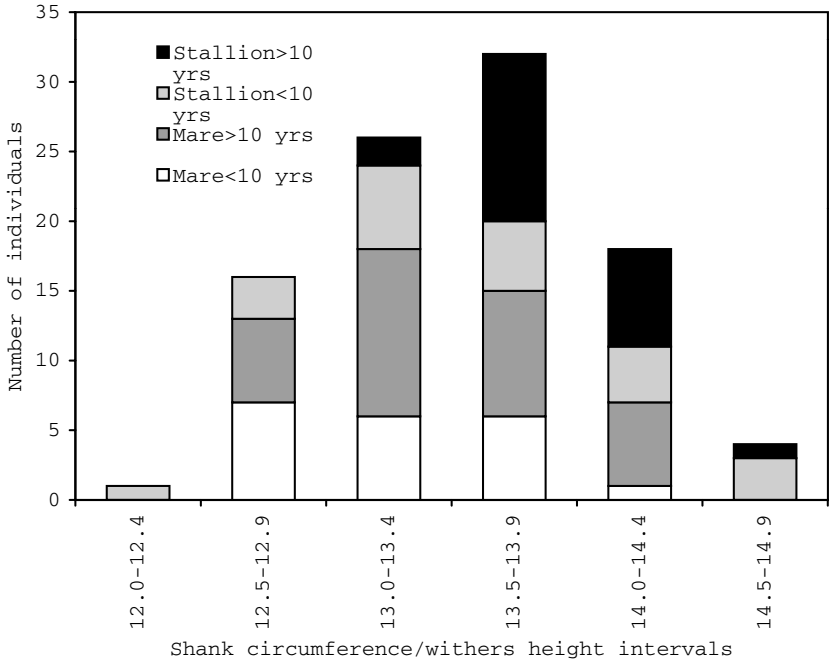


*Fig. 7. The distribution of shank circumference/withers height proportions in Hucul horses by age and sex.*

probably also a stallion. The pelvis bones of the animals are unfortunately totally fragmented, so the conclusions cannot be based on the morphology of these bones. However, the surviving *tuberculum pubicum* in Horse 3 is well-developed, which is characteristic of stallions. The preserved long bones are of no help in solving the problem of sexing: their dimensions also depend on phenotype and age. Only a few data are available to answer this question and most Roman Period horse bones cannot be unambiguously sexed. The metatarsal bones of Horse 2 and 3 fit within the group of modern adult, castrated half-blood horses but do not reach the size of English thoroughbred mares, even though their proportions are similar. To consider the sex of these animals, we can study the morphometry of bones in living specimens of known sex.

The withers heights and shank circumferences (measured in the metacarpal region) of live horses of the unimproved Hucul breed from the Carpathian Mountains (Hankó 1942) show statistically significant differences between mature mares and stallions (Fig. 7). The expression of this difference, however, is aided by the fact that adult individuals of the same breed were available for study. When the ratio of these two body measurements (similar to slenderness indices) is calculated, the difference is still visible in the distribution of individuals of known sex. Unfortunately, when the samples of stallions and mares are combined, this difference is absorbed by major size overlaps between the two groups. This mirrors the situation in archaeozoology, when the sex of animals can only be rarely identified (e.g. on the basis of canines). When the shank circumference/withers height ratios of the pooled Hucul sample and slenderness indices of Roman Period horses are shown side by side, comparable

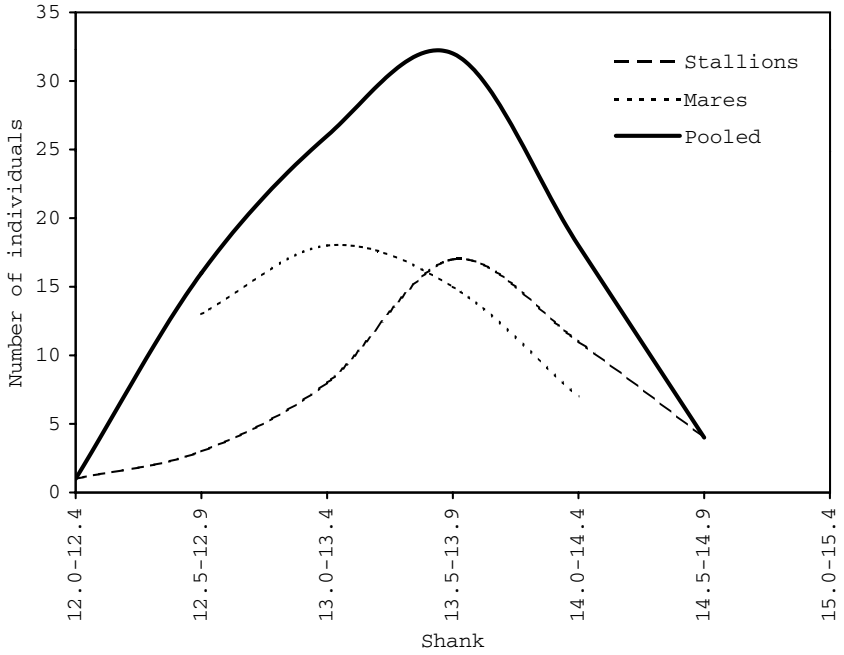


*Fig. 8. The distribution of shank circumference/withers height proportions in the pooled sample of Hucul horses.*

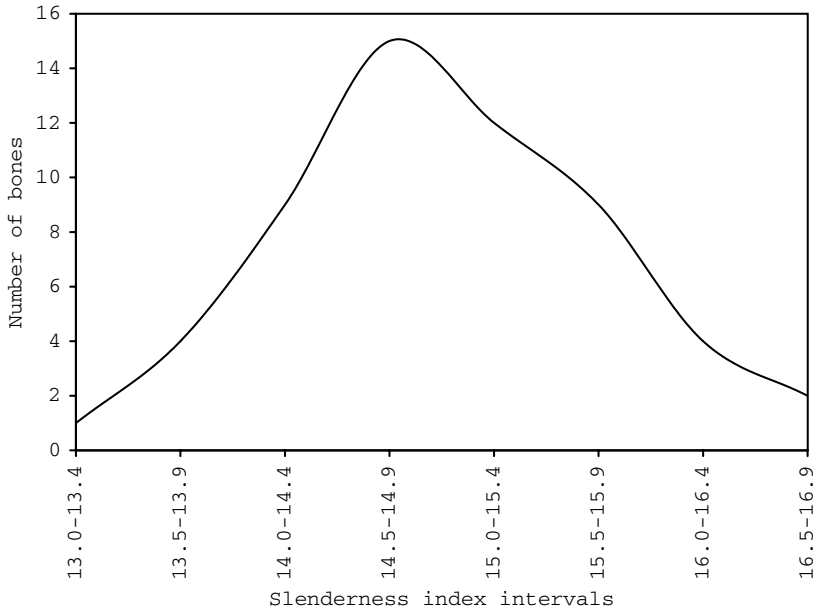


*Fig. 9. The distribution of metacarpal slenderness indices in Roman Period horses.*

(but understandably not identical) normal distributions are obtained (Figs 8 and 9).

The distribution of Roman Period individuals, however, shows a slight asymmetry caused by the presence of relatively broad metacarpal bones. Considering that these more likely belong to stallions than to mares and that the Roman military was indeed rather likely to have used more males and possibly geldings, this difference may cautiously be interpreted as having been caused by sexual dimorphism in the overall Roman Period sample. It must be emphasized, however, that metacarpal broadening is also a consequence of increasing burdening through the animal's life: live weight increases with age until the animal is grown, and the dynamic loading of long bones

*Fig. 10. The equestrian statue of the Roman Emperor Marcus Aurelius: a nice representation of the Roman military horse type.*

also leads to mediolateral broadening. These components all contribute to the phenotype which, in addition is influenced by inherited size ("breed") and environment/keeping conditions that determine its manifestation.

The large sizes of Horses 2 and 3 raise the question of whether they were castrated. Classical authors, e.g. Varro, wrote about the sex of military horses. He stated that military horses were usually not castrated because stallions are more warlike and much stronger than castrated animals (Varro, *Rerum rusticarum de agri cultura, 7*). The pictures and horse-statues from this period that represent military horses, also give the impression of male animals: the neck is usually strong, the breast is wide and the whole body is muscular, like the horses seen on Trajan's column. But it cannot be overlooked that these artistic representations show an ideal horse type worthy of a Roman soldier or leader (Figs 10 and 11).

### *Roman horse "breeds"*

Following comparisons with horse (*Equus przewalskii*) and the unimproved Hucul breed, the Roman horses from Albertfalva could be products of conscious selection that is not necessarily identical with the idea of "breeding" we have today. As mentioned, the horses of Europe became mixed by the Roman Conquest because horses were transferred to different regions of the Empire from its Asian and African provinces. Contemporary authors write about "breeding" and different "horse breeds" but these categories were based on the territories the horses came from, that is, they may rather represent geographical varieties. Ancient authors mention horses from Syria, Trachia, Mauritania, Gallia etc. as different breeds but they do not describe these animals in detail so we cannot come to conclusions concerning their phenotypes. Following Junkelmann (1990), the military horses of the Roman Empire came usually from Thessaly, Thrace, Epirus, Persia, Mauritania, Sicilia, Apulia, Gallia and Hispania. Some Hunnic and Germanic animals were added to this horse stock during Late Antiquity. Three different horse types are described in the book of Flavius Vegetius Renatus, "*Digestorium artis mulomedicinae libri*", used as a "veterinary handbook" in the Roman army. These types include military horses (*proeliis*), racehorses (*circo*) and horses used for travelling (*sellis*). Vegetius Renatus wrote the following about the military horses, "For the purposes of war, the Huns' horses are by far the most suitable, on account of their endurance, working capacity and their resistance to cold and hunger" (quoted by Bökönyi 1974, 267–268). According to Vegetius, Hun horses are followed by Thuringian, Burgundian and Phrygian mounts, similarly unsurpassed in terms of speed and endurance. Finally, war horses from Epirus, the northern Gaul and Dalmatia, "although stubborn, may be reckoned with as very agile in fight" (Vegetius: *Mulomedicina*, III.6.2.; Junkelmann 1990). These sentences also make it clear that the Roman military horse stock was far from homogeneous and probably showed extreme variability, comparable to that of modern horse breeds.

## Discussion

The identification of age, sex and phenotype, based on metapodia alone is difficult and complicated. The variability seen in the record is influenced by many factors and is not necessarily a result of sexual dimorphism and age. Archaeozoological remains often cannot be sexed unambiguously, so to answer this question we have to compare the morphometry of the bones with those of modern specimens. Comparison using modern standards, however, may result in problems (e.g. the Albertfalva horses, probably all stallions, do not attain the dimensions of English thoroughbred mares). Comparisons with primitive types of horses, however, cannot solve these problems either. The average structure of extremities in Hucul and wild horses (*Equus przewalskii*), when compared with that of Albertfalva horses, may express differences that seem to result from sexual dimorphism, even though they are consequences of conscious breeding.

The proportions of bones may help identify the animal's phenotype but one must not forget other factors that affect the bones. Various bones may yield different

*Fig. 11. The representation of two stallions on a Roman mosaic.*

results if compared. Metapodia fuse at a young age, so age differences are not significant in these bones. Since this makes precise ageing almost impossible, we can at best state that a particular specimen was an adult or a young individual.

## Summary

The horses from Albertfalva probably belonged to the Roman military horse type. This "breed" was not homogenous and the newly discovered animals show characteristics of different phenotypes in the skeletal structure of their extremities.

The horses are unfortunately poorly preserved, the skulls and also several of the long bones are completely fragmented. No pathological phenomena were discovered; the synostosis between the two last lumbar vertebrae in Horses 1 and 2 is not pathological: fusion was not accompanied by exostoses and may be considered normal in this region of the vertebral column in mature animals (Bartosiewicz and Bartosiewicz 2002). All three horses were adult animals; Horse 1 died at the age of five years, Horse 2 at the age of eight. Incisior teeth are missing in the case of Horse 3, but the molars which were discovered show that it was an adult as well.

Estimated withers heights, based on the measurable long bones, exceed the Roman average in two of the three horses: 161.7 cm (Horse 2) and 158.6 cm (Horse 3). Horse 1 displays a "standard" size for Roman Period horses (147.3 cm). Metapodial measurements support the theory that the animals were somewhat similar to modern heavy horses on the basis of the diaphyseal width to depth proportions of metatarsal. The slenderness indices, however, are different in Horse 2 and Horse 3; their metatarsal bones nearly reach the slenderness of English thoroughbreds, although are smaller. Metatarsal proportions in Horse 1 are closer to those of other Roman Period military horses and modern half-bred types. Differences are less remarkable between the metacarpal bones: in this sense, all three Albertfalva horses fit within the group of Roman military horses. The radius proportions of Horse 2 and 3 are similar to those of English thoroughbreds and trotters. The radii of Horse 1 are much shorter but the width and the depth reach the values measured on Horses 2 and 3. Horse 1 is probably a typical representative of the Roman military horse; the other two horses were larger, with long and slender limbs.

The well-developed canines in Horse 1 and 2 make it clear that they were stallions or at least geldings; the *tuberculum pubicum* also supports the hypothesis that they were males. Horse 3, on the basis of its size, was probably a stallion as well. Sexual dimorphism in horses is, unfortunately, poorly expressed in the morphometry of long bones. Since metapodials are best preserved, conclusions about sex should be based on these bones above all, but only few data are available to answer this question. The metatarsal bones of Horse 2 and 3 fit within the group of modern adult, castrated half-blood horses, but do not reach the size of English thoroughbred mares, even though their proportions are somewhat similar.

Reconstructing sexual dimorphism from metapodials is difficult, often impossible: aside from sex, there are many other factors such as age, locomotor properties or failures in the limbs that effect metapodial proportions. When the shank circumference/withers height ratios of the primitive Hucul horses and slenderness indices of Roman Period horses are shown together, normal distributions are obtained. The remains of Roman Period horses more likely belong to stallions than to mares and that the Roman military was rather likely to use males and possibly geldings. Differences, therefore, may only cautiously be interpreted as resulting from sexual dimorphism in the Roman Period horse metapodia. We may presume that all three Albertfalva horses were stallions; according to contemporary authors, military horses might not have been castrated.

The three horses whose remains were recovered at

Albertfalva had been probably products of conscious breeding. The horse stock in Europe became mixed during the Roman period: military horses from various areas were transferred to other regions, and some Hunnic and Germanic animals were added during the Late Antiquity, while small, local horse types in various regions were continuously integrated within the population. This mixing caused extreme variability in the horse find material, making the ageing and sexing of bones even more complicated.

*Acknowledgements*

Grateful thanks are due to Dr. Deborah Ruscillo who provided support for the presentation of this paper at the 9th Conference of ICAZ in Durham, UK. Funding for travel to the meetings was provided by the Institute for Aegean Prehistory. Additional thanks go to Prof. Terry O'Connor and an anonymous reviewer for their constructive comments. Comparative data on Hucul horse were contributed by Dr. László Bartosiewicz. The English text was revised by Dr. Alice Choyke.

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*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 247–253*

# 17. Environment, Body Size and Sexual Dimorphism in Late Glacial Reindeer

*J. Weinstock*

*The present study deals with the geographical variation in the body size of reindeer (*Rangifer tarandus*) in western and central Europe during the Late Glacial (*ca. *12–10 ka BP). An osteometrical study of* Rangifer tarandus *revealed that a clear difference in size existed between the populations living in the North European Plain (Britain, northern Germany, and Belgium) and those living in more southern latitudes (southern Germany, Switzerland, and France), with the former being larger. The difference in size however, is not reflected equally in both sexes. Males in both areas commonly reached a similar size; females in the south, however, were usually much smaller than their northern counterparts. This phenomenon could be related to a differing availability of food resources during the summer.*

*This investigation shows that the importance of considering the complexities of body size biology in palaeoenvironmental investigations based on osteometrical data. At the very least, size comparisons between populations of size dimorphic species should be made separately for males and females.*

## Introduction

It has been repeatedly observed that the body size (i.e. body mass) of many species of mammals – e.g. *Cervus elaphus*, *Rangifer tarandus*, *Capreolus capreolus, Sus scrofa*, *Ursus arctos*, and *Vulpes vulpes* – shows marked geographical variation (e.g. Beninde 1937; Herre 1986; Jakubiec 1993). Furthermore, it is also known that the size of some of these and other species – e.g. *Cervus elaphus*, *Rangifer tarandus*, *Megaloceros giganteus*, *Odocoileus virginianus*, *Equus* sp., *Panthera onca*, *Vulpes vulpes*, *Canis dirus* – varied geographically and have fluctuated through time (Davis 1981; Forsten 1993; Guthrie 1984; Kurtén 1984; Lister 1989, 1994; Mariezkurrena and Altuna 1983; Pietschmann 1977; Purdue 1989; Purdue and Reitz 1993; Seymour 1993; Weinstock 2000a).

Since at least the mid 19th century, an attempt has been made to find a causative relationship between this size variability and climatic/ecological factors. Bergmann (1847), emphasizing the thermoregulatory requirements of endothermic animals, postulated a relationship between temperature and body size, with individuals in populations from higher latitudes (i.e. lower temperature) attaining a larger size than those living in lower latitudes (i.e. higher temperature). This relationship, the so-called Bergmann's Rule is often invoked as an explanation for the size variability in some Pleistocene and early Holocene species – a period of repeated climatic and environmental changes (e.g. Davis 1977; Klein 1986; Klein and Scott 1989; Perego *et al.* 2001; Purdue 1980). However, the validity of Bergmann's Rule has been questioned repeatedly (Dayan *et al*. 1991; Geist 1987; McNab 1971). Studies have shown that temperature is not directly responsible in the determination factor of body size. It is nevertheless clear that body size is closely related to physiological and ecologically-relevant variables such as diet – and thus vegetation cover and (indirectly) to climatic factors – population density, and home range size (Calder 1984; Damuth and MacFadden 1990; Schmidt-Nielsen 1984). Thus, understandably, body size has been a focus of many attempts to gain palaeoenvironmental information from osteometrical data (Davis 1977,

1981; Delpech 1983; Mariezkurrena and Altuna 1983; Pietschmann 1977; Purdue 1989; Purdue and Reitz 1993; Seymour 1993).

In the present author's opinion, however these studies fail, not infrequently, to develop their full potential for providing palaeoenvironmental data. One common reason for this is the small number of measurable specimens, which renders size comparisons statistically unreliable. This problem can be circumvented in many instances through the use of index scaling techniques such as the Logarithmic Size Index (LSI) (Meadow 1981, 1984), Variability Size Index (VSI) (Uerpmann 1982; Weinstock 2002), and Relative Size Index (Ducos 1968) – for a review of the techniques see Meadow (1999). These methods have been profitably utilized in studies of Middle Eastern fauna (e.g. Ducos 1968; Ducos and Horwitz 1998; Meadow 1981, 1984; Uerpmann 1979, 1982, 1990; Weinstock 1995) often dealing with the domestication process. With very few exceptions (e.g. Seymour 1993; Weinstock 2002), index-based techniques have not been used on Pleistocene assemblages.

Even when an adequate number of specimens is available, however, some analyses suffer from a failure to consider key aspects of the biology of body size. Especially revealing are studies on strongly size dimorphic genera such as *Cervus*, *Odocoileus*, and *Rangifer* – some of the most common species of wild mammals in Pleistocene and Holocene archaeological sites – as well as *Ursus* and *Panthera*. In many instances, summary statistics for the whole assemblages, i.e. undifferentiated for males and females, are used to compare between geographical areas or periods (Delpech 1983; Mariezkurrena and Altuna 1983; Pietschmann 1977; Purdue 1989; Seymour 1993). The problem with this approach is of course that the proportions of males and females of a species may, and commonly does, vary from site to site (e.g. Weinstock 2000a, c), and this will strongly influence the resulting 'mean' size for a given site. Therefore, the distribution of the data rather than the basic statistical parameters (e.g. mean, standard deviation) is much more useful for this purpose. In addition, some of the complexities of the biology of body size are sometimes overlooked, leading to potentially misleading conclusions.

In a recent paper on the size decrease of *Odocoileus virginianus* in the southeastern USA during the Holocene, the authors found a lack of concordance between the size changes in males and females. They found this troubling and ascribed it to low number of measured specimens in some of the samples analysed (Purdue and Reitz 1993). I would argue that such a lack of concordance is to be expected in sexually dimorphic polygynous ungulates. This contribution attempts to prove this assertion through the analysis of the geographical variability of body size of reindeer (*Rangifer tarandus*) during the Late Glacial (*ca.* 12–10 ka BP).

## Material and Methods

The osteometrical material in this study comes from a number of sites in western and central Europe (Fig. 1): areas sampled included northern Spain, the Paris Basin, the Périgord region in southern France, Great Britain, Belgium, northern and southern Germany and Switzerland. All sites belong to the Late Glacial (*ca.* 13–10 ka BP), and most date to the Bölling/Allerød 12.5–12 ka BP. Most measurements were taken by the author following von den Driesch (1976), though a number of additional depth measurements were defined (Weinstock 2000a). Only post-cranial material of individuals in age stages where the sexual dimorphism in reindeer is well developed, i.e. adults and older subadults, was measured. This includes specimens with all their epiphyses fused and, for proximal humerus, proximal and distal femur and proximal tibia, specimens with epiphyses in the process of fusing (Weinstock 2000b). Specimens of juvenile and immature animals (epiphyses unfused) were disregarded. Dental data were ignored because they are not as closely correlated with body size (Dayan *et al.* 1991; Herre 1951; van Valkenburgh 1990). Similarly, length parameters of long bones, while possibly indicative of the 'build' of an animal, are not very closely correlated with body mass (Scott 1985, 1990) and therefore were not included.

In investigations of body size, it is important to work with large samples of measured specimens and therefore an index-based method; the Variability Size Index or VSI (Uerpmann 1982; Weinstock 2002) was utilized. As mentioned above, index-based techniques allow different skeletal elements to be pooled together, thus resulting in a much larger sample size than would be the case when working with single skeletal elements (Meadow 1999). The basic idea behind these methods is to relate the dimensions of a paleontological or archaeological specimen to those of a standard of the species being investigated. In the case of the VSI, the standard is not a single individual (as in the Logarithmic Size Index or LSI) but a 'population'. The latter may consist of a large series of skeletons, either recent or archaeological, belonging to a more or less closed population, or of a large number of bone fragments recovered from a well-defined temporal unit in an archaeological/paleontological site. Following this method, an index is built for each of the dimensions of a fragment according to the formula

$$\mathrm{VSI} = \frac{x-m}{2s} * 50$$

where $x$ is the actual measurement for which the index is being calculated, $m$ is the arithmetical mean of the standard population for that dimension, and $s$ is the standard deviation of the standard population for the dimension in question (Uerpmann 1982). From all indices calculated for a specimen, an arithmetical mean is built, resulting in a 'mean VSI' for that specimen. This index

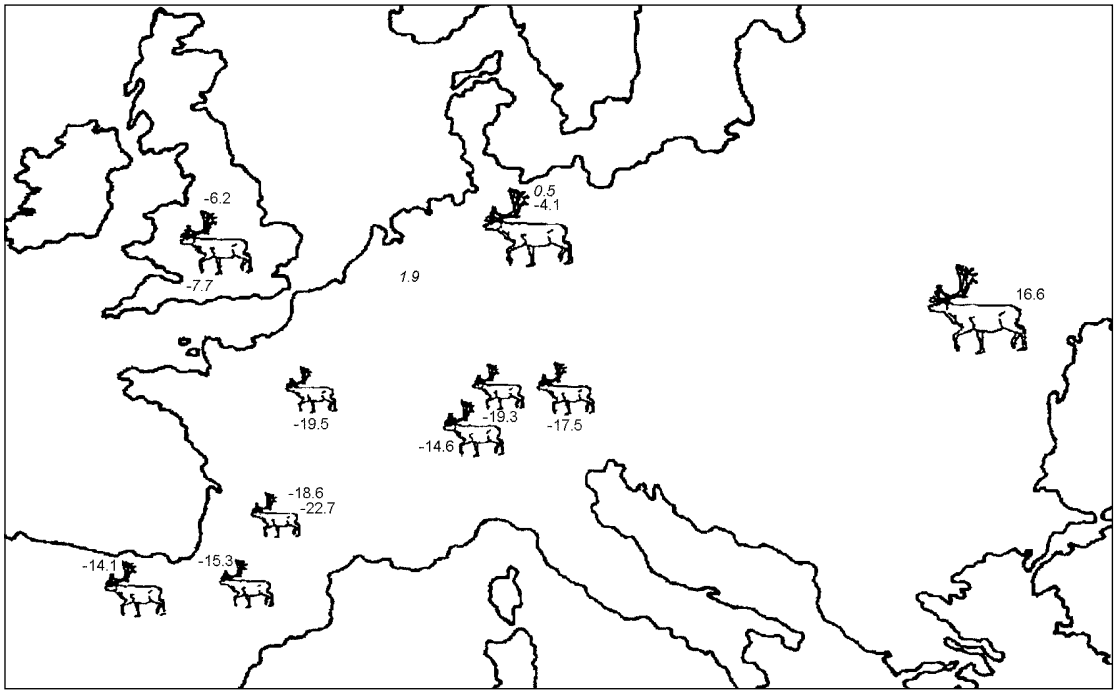


*Fig. 1. Mean VSI indices in each of the investigated sites. Figures in normal font represent sites dating to the Bölling/ Allerød (*ca. *12.5–11 ka BP), italics represent sites dating to the Younger Dryas (*ca. *10 ka BP).*

is positive if the fragment is larger than the mean of the standard population and negative if smaller.

For this study, the standard population was built with the reindeer material from the Late Glacial Ahrensburgian layer (*ca.* 10 kyr BP) of Stellmoor, an open-air site near Hamburg in northern Germany (Rust 1943). Apart from its excellent state of preservation, it is very rich – more than 20,000 bones were recovered, from which 1803 specimens were measured for this study – and was deposited within, archaeologically speaking, a very limited period of time (Gronnow 1987; Bratlund 1991; Bokelman 1991; Weinstock 2000a, 2000b; for a detailed discussion of this 'standard population' see Weinstock 2000a).

## Results

If the mean body size of reindeer, as represented by the mean value of the VSI indices, is considered, a basic pattern is apparent: reindeer in northern latitudes (northern Germany, Belgium, Britain) were larger (less negative VSI indices) than those in more southerly latitudes (northern Spain, France, southern Germany, Switzerland), although some variation exists within these two groups as well (Fig. 2, Fig. 1). One could argue that this North/South (N/S) size difference is in accordance with Bergmann's Rule, and that lower temperatures in the north are the reason for this pattern. This, however, would be misleading. A look at the *distribution* of the VSI of sites with more than 100 measurable specimens (Fig. 3) suggests that the situation is more complex than that. The upper range of the variation (i.e. the maxima) in sites in the southern group is not very different than in the northern group. In contrast, the lower range of the distribution (i.e. the minima) of both groups is very different. It is striking, for example, that among the *ca*. 1800 specimens measured from the Ahrensburgian layer of Stellmoor in northern Germany, none reaches a VSI minimum near that of the Swiss site of Kesslerloch (N=1384). By plotting the relative *frequencies* from contemporaneous sites (Bölling, *ca.* 13–12 ka BP) – the Hamburgian layer from Stellmoor and the neighbouring site of Meiendorf in northern Germany and Schussenquelle in southern Germany – it can be shown that the very low minima of the southern sites are not due to isolated anomalous values (Fig. 4). Both assemblages show a bimodal distribution. Given the large degree of size dimorphism in *Rangifer* and the fact that no juveniles were included in the study, one can safely assume that the left and right peaks in the curves represent females and males respectively. It is clear that while the male peaks of both curves do not differ much, the female peak of the Schussenquelle is displaced to the left in relation to that of the northern German sites, pointing to the smaller size of the females in southern Germany. In other words, there was a larger degree of sexual dimorphism in reindeer populations in the southern

| Site | mean | s | min | max | n |
|---|---|---|---|---|---|
| *Spain and southern France* | | | | | |
| Northern Spain* | -14.17 | 30.92 | -55.72 | 31.15 | 9 |
| Dufaure 4[1] | -15.38 | 25.23 | -101.05 | 53.91 | 116 |
| Gare de Couze H* | -22.70 | 23.47 | -66.2 | 49.43 | 60 |
| La Madeleine (Excav. 1865)* | -18.69 | 21.14 | -68.51 | 31.95 | 205 |
| Gare de Couze G* | -18.00 | 23.8 | -99.84 | 52.58 | 238 |
| Veyrier[2] | -14.62 | 26.99 | -114.22 | 33.53 | 74 |
| *Paris Basin* | | | | | |
| Pincevent[3] | -19.51 | 35.18 | -130.74 | 88.11 | 606 |
| *Southern Germany and Switzerland* | | | | | |
| Schussenquelle* | -17.51 | 27.27 | -89.2 | 48.35 | 209 |
| Petersfels* | -22.41 | 28.31 | -103.21 | 63.29 | 158 |
| Kesslerloch* | -19.33 | 25.89 | -113.69 | 62.24 | 1384 |
| *Lower Rhine Valley* | | | | | |
| Andernach[4] | -13.73 | 43.18 | -57.41 | 62.3 | 6 |
| *Great Britain* | | | | | |
| Kent's Cavern* | -7.78 | 21.73 | -41.94 | 29.32 | 23 |
| Ossom's Cave* | -6.21 | 33.78 | -74.47 | 62.5 | 28 |
| *Northern Germany and Belgium* | | | | | |
| Stellmoor HL + Meiendorf* | -4.11 | 25.42 | -58.6 | 77.81 | 330 |
| Stellmoor AL* | 0.51 | 23.29 | -53.21 | 70.49 | 1803 |
| Hohler Stein[5] | -2.84 | 22.64 | -36.06 | 49.92 | 25 |
| Remouchamps[5] | 1.97 | 27.04 | -60.5 | 50.39 | 27 |

*Fig. 2. Statistical summary of VSI values in the sites examined for this study.* measured by author; [1] Altuna* et al. *1991; [2] Koenig and Studer 1981; [3] J. Enloe, pers. comm.; [4] M. Street pers. comm.; [5] Baales 1996.*

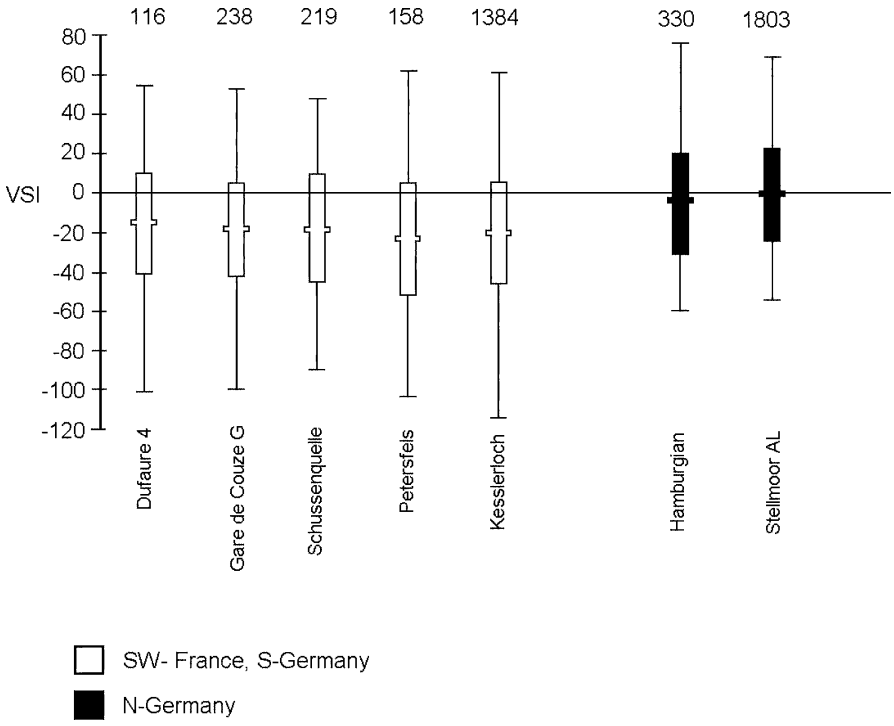


*Fig. 3. Distribution of Variability Size Indices (VSI) in 'southern' and 'northern' sites. Only sites with N>100 plotted. (Pincevent not included because bones of juveniles from this site were measured and the smallest specimens may belong to this age class.)*

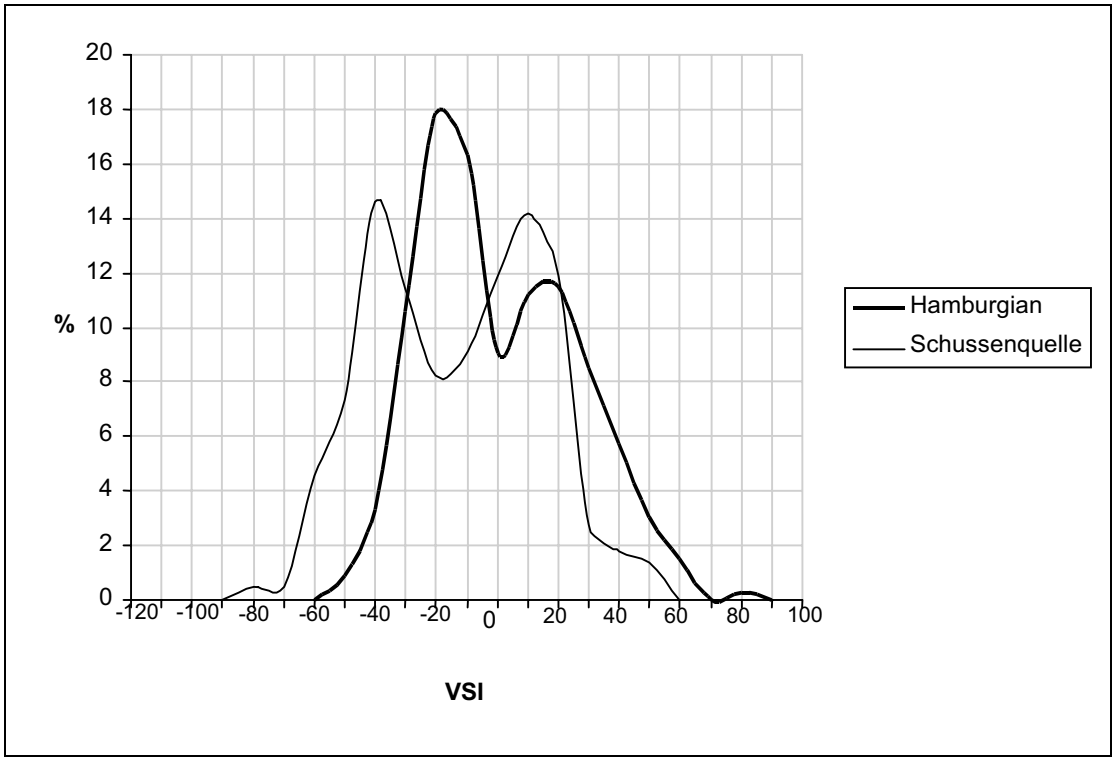


*Fig. 4. Frequency of VSI indices in a south-German site (Schussenquelle) and in north-German 'site' (Hamburgian = Stellmoor and Meindorf).*

'group'; females in this group were considerably smaller than those in the north whereas the size of males in both groups did not differ much.

## Discussion

Such a pattern (i.e. difference in degree of size dimorphism) cannot be explained by differences in temperature (i.e. Bergmann's Rule). An alternative explanation must therefore be sought. In all probability, the answer lies in the fact that the selective forces acting upon males from most species of polygynous ungulates, *Rangifer* included, are different from those acting upon the females. This is a result of the different reproductive strategies and investment of both sexes (Clutton-Brock *et al*. 1982). In order to mate, males have to fight amongst each other for the access to females, and in this struggle a large body size and large antlers bestow a great advantage. Thus, a selection for heavier, large-antlered males is to be expected (Clutton-Brock *et al.* 1982). Obviously, environmental constraints still impose limits to maximal male adult body size. On the other hand, the adult body size of females depends on whether growth is continued after maturity (Skogland 1983, 1989). Studies on modern wild Norwegian reindeer have shown that under conditions of food abundance females continued to grow after maturity. Under food limitation, however, females increased their reproductive efforts by having their own somatic growth arrested. Thus, "… the degree of sexual dimorphism [will] be enhanced by food limitation, given that males put a premium on developing large size to be a successful breeder, while female success is measured in terms of lactation" (Skogland 1989, 10).

Thus, the hypothesis put forward here is that the larger degree of sexual dimorphism evidenced by reindeer living in more southerly regions of western and central Europe during the Late Glacial was a product of their living under conditions of relative food limitation. This food limitation must have occurred during the summer, the season in which animals obtain the protein necessary for somatic growth. Food limitation during the summer has been related to small size of animals in modern populations of reindeer *Rangifer tarandus*, white-tailed deer *Odocoileus virginianus*, and moose *Alces alces* (Hjeljord and Histol 1999; Lesage *et al*. 2001; Skogland 1989). The cause(s) for the food limitation in the south must still be determined. Differences between the vegetation cover in northern and southern Europe during the Bölling (*ca*. 13–12 ka BP, uncalibrated) have been determined through palynological evidence. In the course of this period, the soil in northern Europe, an area formerly under the ice sheets, stabilized and this, together with an increase in precipitation, allowed the development of a

shrub-tundra with dispersed tree birch (*Betula pubescens*) and some juniper (*Juniperus*) and willow (*Salix*). In the south, in contrast, proportions of arboreal pollen of up to 30–50% – mostly juniper – have been recorded (Frenzel 1983; Paquereau 1976). The difficulty however, is to correlate these differences with the specific differences in the diet of reindeer in both areas during the growing season. An alternative explanation would be that harsher winters in the northern area caused heavy winter mortalities (relatively to those in the south), resulting on increased quantity and quality of available growth fodder per individual during the following growth season (Guthrie 1984) and, correspondingly, a larger body size. It is a well-known principle among wildlife managers that a reduction through hunting of a herd of deer during the non-growth season results in an increase of the individual deer quality (Klein 1965, 1985). In other words, the difference in body size may have been a result in differences in population density.

## Conclusion

It is hoped that this contribution has shown the potential of "body size" as a source of palaeoenvironmental information. In order to exploit this variable with maximum profit, however, the complexity inherent in this parameter must be taken into account. For sexually dimorphic species, this includes the different selection pressures acting upon each sex. At the very least, when comparing the size of sexually dimorphic species, males and females should be treated separately. It is suggested that methods should be used that increase the effective size of the samples to be compared. Despite some problems with the index-based methods, they have proven invaluable in the study of assemblages that have only a limited number of measurable bones.

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*Recent Advances in Ageing and Sexing Animal Bones (ed. Deborah Ruscillo) pp. 254–261*

# 18. Sexual Dimorphism in the Postcranial Skeleton of European Fossil Elephants

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*The fossil elephants of two contemporaneous phylogenetic lines were widely distributed in Europe during the late Pliocene and Pleistocene. The mammoth lineage was represented by three main nominal chronospecies: the southern mammoth (*M. [Archidiskodon] meridionalis*, Nesti), the steppe-mammoth (*M. trogontherii*, Pohlig), and the woolly mammoth (*M. primigenius*, Blumenbach). The only representative of the second elephant lineage is the forest or straight-tusked elephant (*Palaeoloxodon antiquus*, Falconer and Cautley).*

*Sexing skeletons of fossil elephants is important for understanding aspects such as the taphonomy of sites, interpretation of size or social structure. The high degree of accuracy in sex determination for fossil elephant is given by considering series of features in the whole skeleton. The skull and tusk morphology is of great value for separating male and female adult animals, but most discoveries include separate bones with these elements lacking. In addition to sexual dimorphism in the cranial material, the postcranial bones provide information for sex determination, as former studies have shown for some fossil or living elephants. This study was undertaken to establish the diagnostic biometrical and morphological features of postcranial skeleton of three European fossil elephants for sex determination. This information could contribute to future works in determining the sex of individuals from separate bones.*

## Introduction

The determination of sex ratio of proboscideans in fossil assemblages is very important for understanding the taphonomy of sites, interpretation of size, and other features of individuals that may be affected by sexual dimorphism. The sex ratio and age structure of a population provide information about the paleobiology and paleoecology of extinct species.

Sex determination relies on several criteria: in exceptional cases, on well preserved soft tissue of genitals (Averianov 1996, Garutt 1964), morphology of skull and tusk, size and robusticity of long bones, and morphology of pelvis.

The dimension of tusks and their alveoli are of great value for separating male and female animals. The measured diameter of the tusk base and/or maximum length is most useful. Males' tusks are larger and more massive overall, while those of females are smaller, straight and more gracile. This difference is also reflected in the morphology of the tusk alveoli of the skull, which tend to be broader and more divergent in males than in females (Lister and Agenbroad 1994). This method is complicated by great age variation, which must be taken into consideration.

Elephants are very dimorphic species, and males are usually much heavier than females. This is reflected in osteometric data of bones, but not all elements show the same degree of dimorphism. Osteometric data of the bone remains, especially of long bones, can provide valuable information on sex ratio. In general, sex determination on long bones is based on the fact that males are much taller than females, because their epiphyses fuse at an older age and their total growth is much greater (Haynes 1991). Therefore, it is necessary to use the bones with

fused epiphyses, omitting males which have not attained a final state of skeletal fusion whose size, thus, can be similar to adult females.

Similarly, the stronger cervical muscles and thus the cervical vertebrae to support the higher weight of tusks of males are also reported to be dimorphic between the sexes (Averianov 1996). Averianov reports a relatively larger atlas and axis, specifically the robust dorsal tubercle on the *arcus dorsalis* (atlas), and an extensive sculpture on the axis in males.

Another criterion for sex determination is the most often used pelvic morphology. The pelvis of the female is hormonally influenced during the life and to an increased degree during pregnancy – the bone is resorbed along the pelvic aperture to widen the birth canal. The inner boundary of the aperture is emphasized with successful pregnancy, the *corpus ossis ilii* becomes thinner and the *eminentiae iliopubicae* become enhanced (Kroll 1991). The basic difference between males and females is a relatively smaller "birth canal" and relatively broader ilium in males than in females.

## Material and Methods

The bone material selected for this investigation comes from several localities. The samples were chosen in such way as to show representatives of three European elephant species from important localities. The species *Mammuthus trogontherii* was left out because of its small minimum count of excavated postcranial bones at appropriate sites. *Mammuthus meridionalis* remains come from Upper Valdarno (late Villafranchian) in Italy, which is the type locality of this species (Azzaroli 1977). The sites Milovice and Předmostí (upper Pleistocene, dated on average to 26 kyr BP) in the Czech Republic have provided *M. primigenius* remains. They are located on the slopes of the Pavlovské Hills above the Dyje River (Milovice) and in the SW part of the so-called Moravian Gate pass (Předmostí). The collection of remains of *P. antiquus* are housed in Bilzingsleben (east Germany), and they were found near Frankleben, dating to the middle Pleistocene. Several individuals of this species from Upper Valdarno were also included in the investigation, but in contrast to *M. meridionalis*, these bones are from more recent layers (middle Pleistocene).

In the postcranial skeleton, the pelvic morphology is the most obvious anatomic site for sexual dimorphism, as mentioned above. The most important measurement is the width of pelvic aperture. In a complete pelvis, the size of the aperture is quantified in its greatest width (Lister and Agenbroad 1994, Lister 1996b). The ilium width estimation is more complicated. The *ala ossis ilii* width is apparently dimorphic, but this part of the skeleton is strongly influenced by the form and size of its lateral segments (*tuberositas iliaca*) which are very variable and not necessarily dependent on sex. Consequently, the other extent of the ilium is used in this study (see below). The most suitable measurement is repeatable and reflects increased robusticity of the ilium in males. The measurement at the constriction of the shaft above acetabulum at its narrowest point meets these requirements, and is commonly found intact in deposits (Lister 1996b). However, for the present study, the maximum acetabulum length of the ilium defined by Duerst (1926) was used. Lister (1996b) and Göhlich (2000) showed that none of these single measurements are enough for sexing between males and females: there is often overlap in the ranges of the two sexes. The most reliable separation is given by the index between the width of pelvic aperture and the length of acetabulum.

In this study, the sex of the above mentioned skeletons was determined on the basis of the pelvic morphology in animals where the ilium was complete or partially preserved. This primary sexing information was then used for examining sexual dimorphism in the long bones, the atlas and the axis of the same skeleton. The long bones of the specimens of known sex, independently from the pelvis, have been plotted on bivariate graphs, together with samples including individuals of undetermined sex. The bivariate plots should ideally show the bimodal distribution of two well-defined sex groups. Thus the number of males and females could theoretically be determined directly from the graphs. In addition to the material mentioned above, additional data from several publications were added to the graphs. A complete pelvis from *M. primigenius* was not available, thus sex separation in long bones had to be based on published datam where the sex of the specimens was already determined from body size, skeletal robusticity, and pelvic shape. Plotting miscellaneous specimens of *M. primigenius* gives a wide range of male and female clusters because this species varied considerably in body size through time and space (Lister 1996a).

Only the adult bones with fused epiphyses were chosen for comparison, but this reduced the sample size, especially the remains from the localities Milovice and Předmostí. The bones were measured following the definition of Duerst (1926). The measurements were undertaken in a standardized pattern. For all the limb bones, the length was always measured in proximal-distal direction, the width in a medial-lateral direction, the height in a proximal-distal direction, and the depth in anterior-posterior direction.

The samples studied by the author, were examined using additional comparative measurements. The comparative data were taken from the literature, except individuals found in Siberia, where the measurements of ulna were taken directly by the author. Unfortunately, the Siberian sample lacks precise find location. In the comparisons, the following (partial) skeletons or individual bones are included: samples of species *P. antiquus*

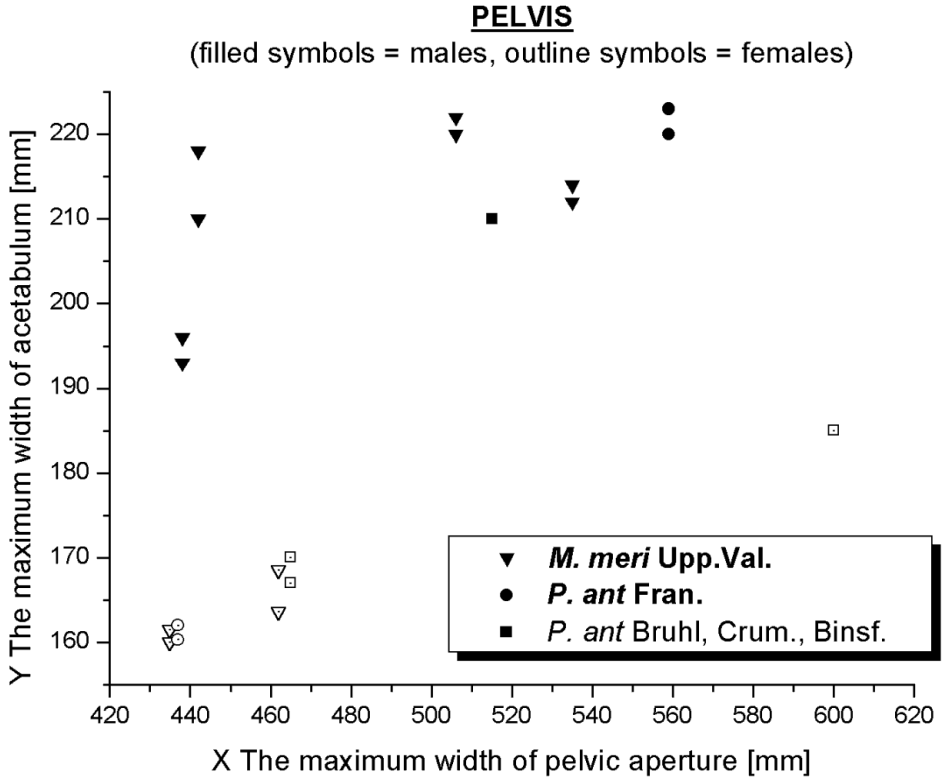


*Fig. 1. Scatter diagram of pelvic aperture width versus acetabulum width;* M. meri *Upp. Val.* = Mammuthus meridionalis *from Upper Valdarno;* E. ant *Fran.* = Palaeoloxodon antiquus *from Frankleben;* E. ant *Bruhl, Crum.* = P. antiquus *from Brühl and Crumstadt.*

from Crumstadt (Germany, Kroll 1991), Brühl-Kiesäcker and Binsfeld (Germany, Göhlich 2000), Ciechanów, Józwin, Warsaw, Gröbern, Grabschütz (Poland and Germany, Jakubowski 1996). Samples of the species *M. primigenius* are from Rottweil, Ahlen, Polch, Siegsdorf, Steinheim, Pfännerhall (Germany, Ziegler 2001), Stuttgart, Borna, Niedzica and Starunia (Germany, Poland and Ukraine, Kulczycki 1955).

## Results

It was not possible to take measurements of all specimens on the pelvis due to fragmentation, however, the aperture width and the acetabulum length could be measured on eight partial or complete pelves. Another three pelves (females from Crumstadt and Binsfeld, male from Brühl-Kiesäcker, Germany, Göhlich 2000) were added from the literature for comparison with author's results. Their measurements are plotted in Fig 1 and demonstrate a bimodal distribution (females and males are separated). Proportions between measurements therefore provide a clear distinction between the sexes. According to the bivariate plot of the pelvis, males from Upper Valdarno are more numerous than females, i.e. four males and two females. All except two of the Upper Valdarno specimens were also sexed by Lister (1996b) (IGF-14838, IGF-10791, IGF-1050, IGF-13730) who came up with the same result, including redetermination of specimen IGF-14838 as male, previously identified by Azzaroli (1977) as female. It was not possible to determine the same information on the specimens from Frankleben because of the small number of their pelves. The comparison of proportions in this species (my own and additional measurements) gives a less clear separation between two sexes, but the ratios do not overlap in the ranges of males and females, at least as far as sample sizes allow. The ratios between aperture width and acetabulum length give values ranging between 2.45–2.54 in males and 2.7–3.2 in females. Although the pelvic sample of *P. antiquus* is very small, the specimens available suggest that the gender distinction may be valid for this species too, as Göhlich (2000) has already shown. On the other hand, both Maria-Rita Palombo (Italy) and Paul Davies (UK) have indicated that the method does not work on sexed *Palaeoloxodon* material from their countries (Lister, pers. comm.).

Each of the measurements on long bones was first plotted on bivariate axes to test for sexual dimorphism using specimens of known sex, independently of the pelvic

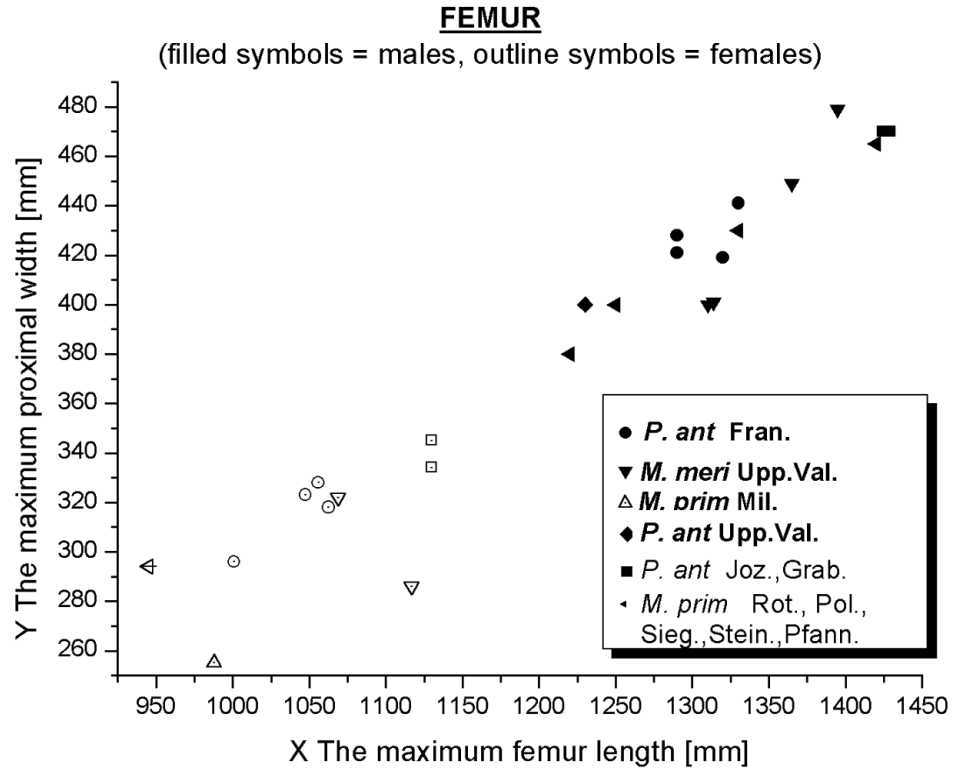


*Fig. 2. Scatter diagram of maximum femur length versus maximum proximal width;* E. ant *Fran.* = Palaeoloxodon antiquus *from Frankleben;* M. meri *Upp. Val.* = Mammuthus meridionalis *from Upper Valdarno;* M. prim *Mil.* = Mammuthus primignius *from Milovice;* E. ant *Upp. Val.* = P. antiquus *from Upper Valdarno;* E. ant *Joz., Grab.* = P. antiquus *from Jóźwin and Grabschütz;* M. prim *Rot., Pol., Sieg., Stein., Pfann.* = M. primigenius *from Rottweil, Polch, Siegsdorf, Steinheim and Pfännerhall.*

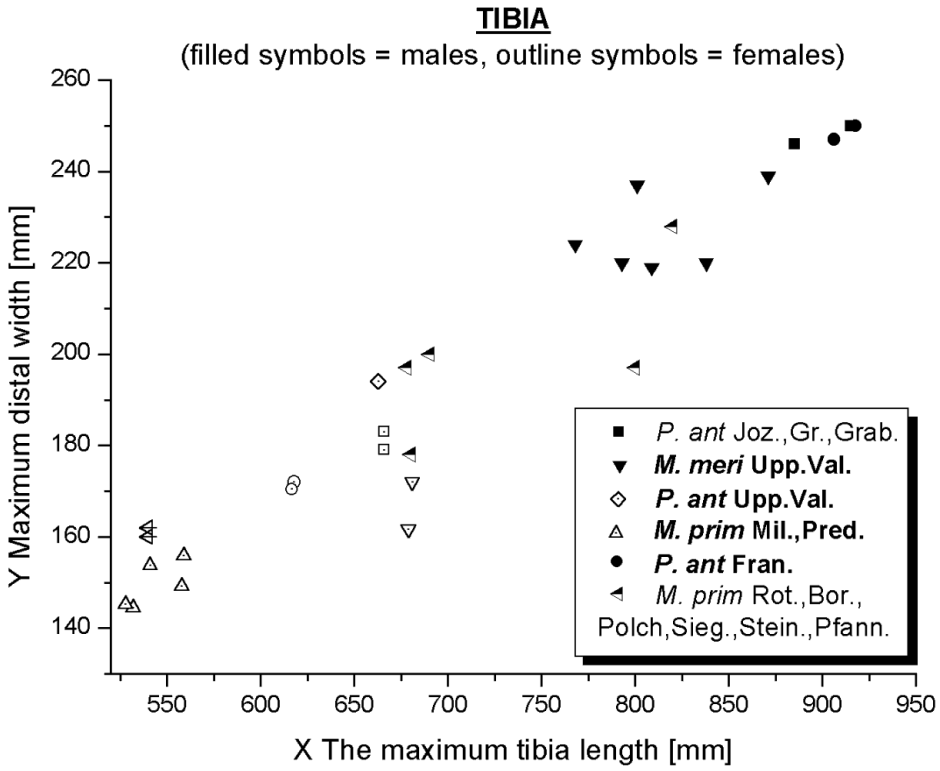


*Fig. 3. Scatter diagram of maximum tibia length versus maximum distal width;* E. ant *Joz., Gr., Grab.* = Palaeoloxodon antiquus *from Jóźwin, Gröbern and Grabschütz;* M. meri *Upp. Val.* = Mammuthus meridionalis *from Upper Valdarno;* E. ant *Upp. Val.* = P. antiquus *from Upper Valdarno;* M. prim *Mil., Pred.* = Mammuthus primigenius *from Milovice and Předmostí;* E. ant *Fran.* = P. antiquus *from Frankleben;* M. prim *Rot., Bor., Polch, Sieg., Stein., Pfann.* = M. primigenius *from Rottweil, Borna, Polch, Siegsdorf, Steinheim and Pfännerhall.*

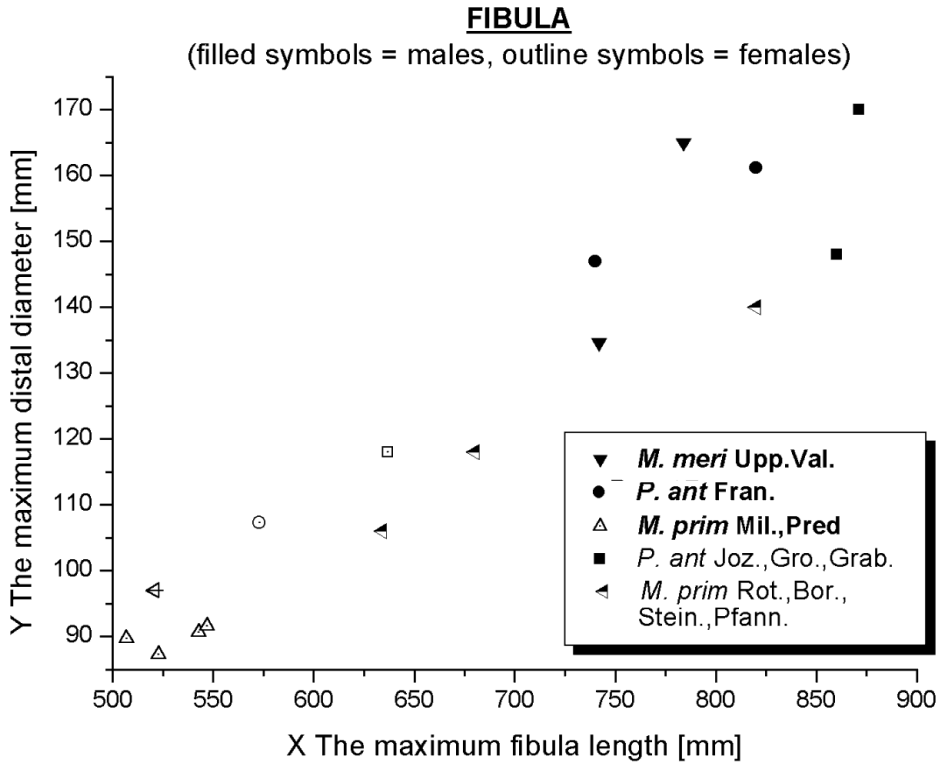


*Fig. 4. Scatter diagram of maximum fibula length versus maximum distal diameter;* M. meri *Upp. Val.* = Mammuthus meridionalis *from Upper Valdarno;* E. ant *Fran.* = Palaeoloxodon antiquus *from Frankleben;* M. prim *Mil., Pred.* = Mammuthus primignius *from Milovice and Předmostí;* M. prim *Rot., Bor., Stein., Pfann.* = M. primigenius *from Rottweil, Borna, Steinheim and Pfännerhall.*

information. After inclusion of samples of undetermined sex, the graphs showed sex ratios within species from the studied localities. It must be stressed that it is necessary to look and assess measurements of species separately in the graphs, because of considerabe size difference of studied species.

In the femur, a plot of the proximal width against the maximum length (Fig. 2) indicates that males from Upper Valdarno were more numerous than females, i.e. five males and two females; one sample from this skeletons belongs to a male of *P. antiquus*. Data from Frankleben suggest a more or less even distribution of two sexes, i.e. four males and four females. The only adult femur comes from Milovice, whose very small size argues strongly in favour of a female identification. The bivariate plot of the distal width against the maximum length of tibia (Fig. 3) also reveals a bimodal distribution. The plot again shows a higher abundance in bones of males from Upper Valdarno, i.e. six males and two females of *M. meridionalis*, and one probable female bone of *P. antiquus*. Two male tibiae and two female tibiae are from Frankleben. There are only females (five individuals) at the sites of Milovice and Předmostí the sample contained no remains of males. The plots of fibula, humerus, radius and ulna (Figs 4–7) illustrate similar sex ratios for *M. meridionalis* and *M. primigenius*, namely a dominant representation of male remains from Upper Valdarno and probable absence of male remnants from the localities of Milovice and Předmostí. On the other hand, the plots of these four bones reveal more numerous males than females in *P. antiquus* from Frankleben.

In summary, plots of long bones suggest the following sex ratios: dominant representation of male skeletons of *M. meridionalis* from Upper Valdarno, slightly dominant representation of male skeletons of *P. antiquus* from Frankleben, and an absence of male skeletons of *M. primigenius* from Milovice and Předmostí. It must be stressed that this result is based on adult animals only of very small sample sizes.

Differences between males and females were not found in the atlas and axis. As a consequence of different size, bivariate plots of *arcus dorsalis* against the maximum width of both vertebrae show partial separation between males and females, but no distinct groups are apparent (Averianov 1996). The reason for the lack of complete separation in the two groups may be attributed to the possible presence of immature and/or subadult males, which are not easily distinguished from adult females, as

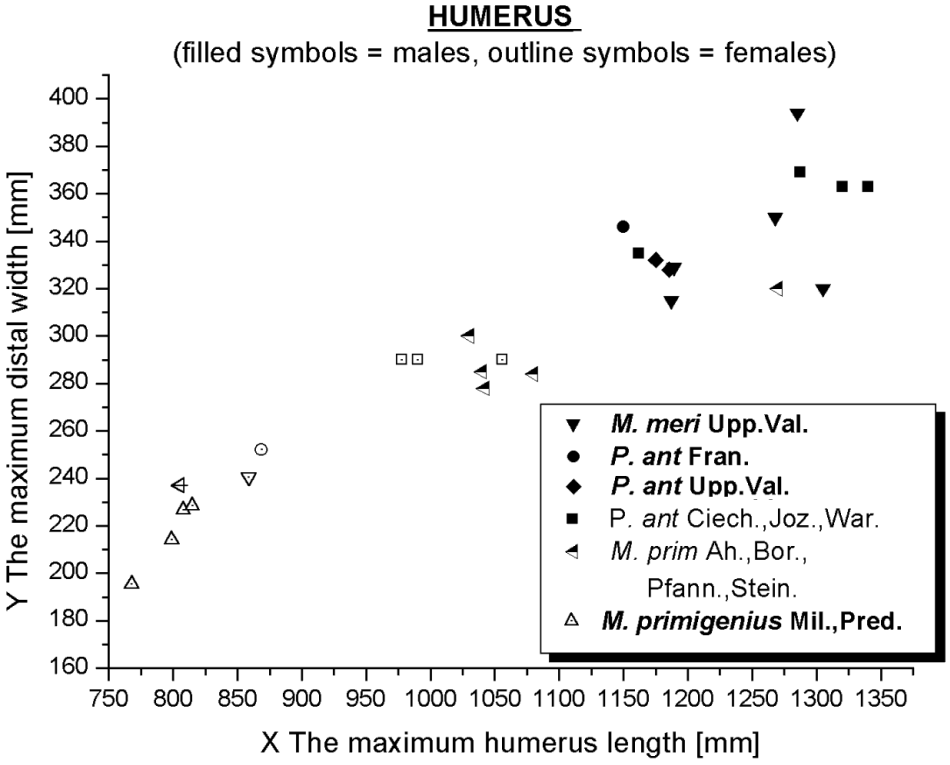


*Fig. 5. Scatter digram of maximum humerus length versus maximum distal width;* M. meri *Upp. Val.* = Mammuthus meridionalis *from Upper Valdarno;* E. ant *Fran.* = Palaeoloxodon antiquus *from Frankleben;* E. ant *Upp. Val.* = P. antiquus *from Upper Valdarno;* E. ant *Ciech., Joz., War.* = P. antiquus *from Ciechanów, Jóźwin and Warsaw;* M. prim *Ah., Bor., Pfann., Stein.* = Mammuthus primigenius *from Ahlen, Borna, Pfännerhall and Steinheim;* M. prim *Mil., Pred.* = M. primignius *from Milovice and Předmostí.*

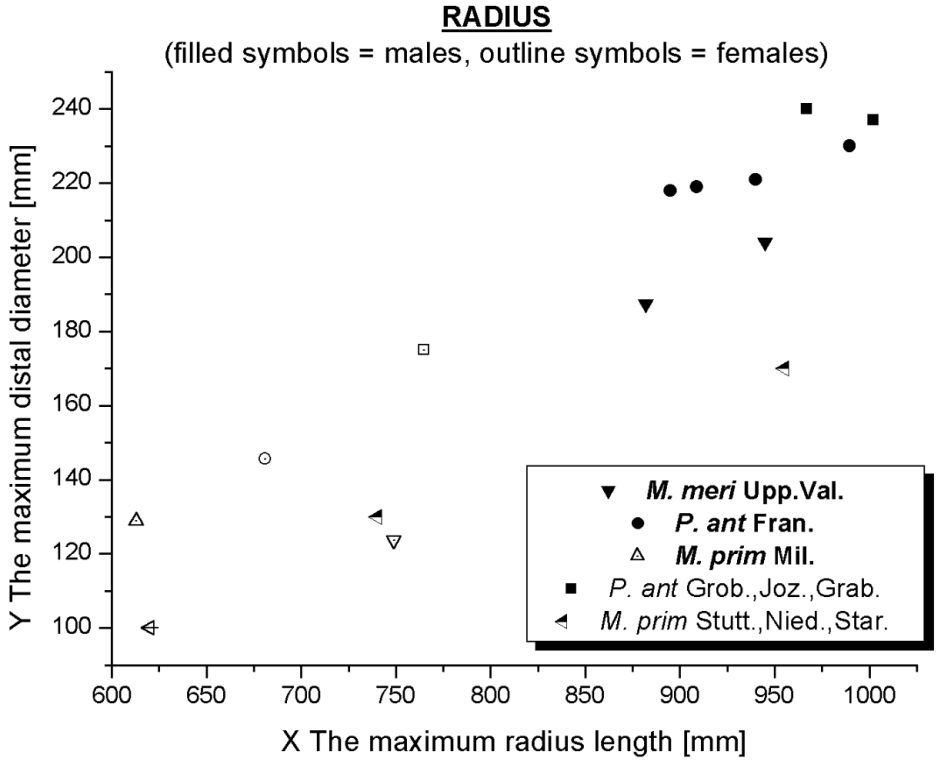


*Fig. 6. Scatter diagram of maximum radius length versus maximum distal diameter;* M. meri *Upp. Val.* = Mammuthus meridionalis *from Upper Valdarno;* E. ant *Fran.* = Palaeoloxodon antiquus *from Frankleben;* M. prim *Mil.* = Mammuthus primignius *from Milovice;* E. ant *Gro., Joz., Grab.* = P. antiquus *from Gröbern, Jóźwin and Grabschütz;* M. prim *Stutt., Nied., Star.* = M. primigenius *from Stuttgart, Niedzica and Starunia.*

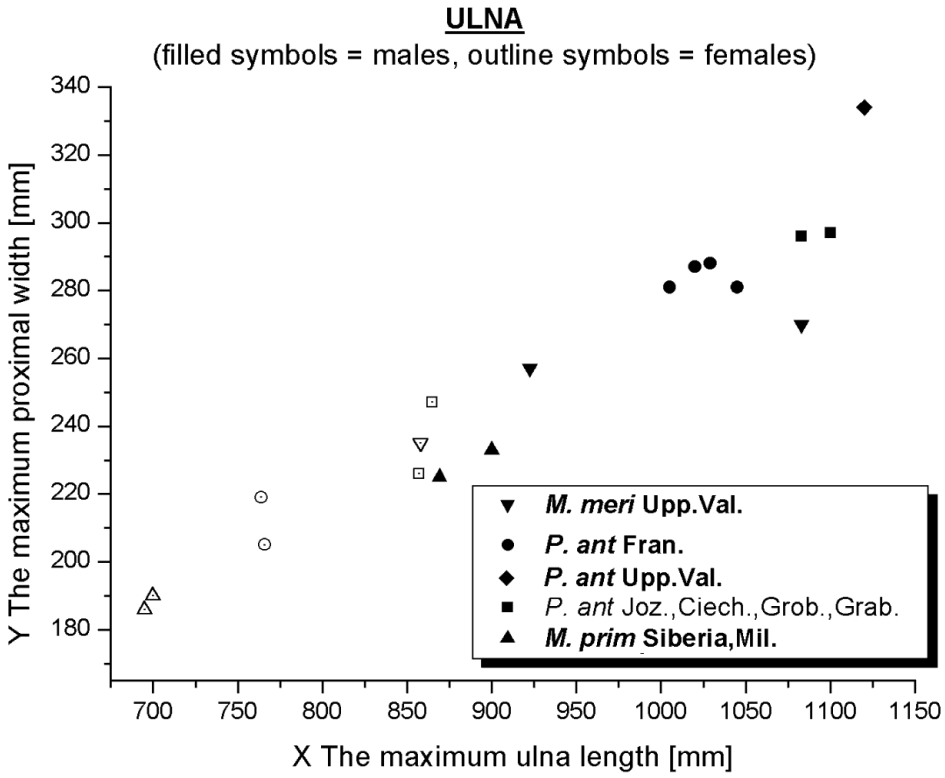


*Fig. 7. Scatter diagram of maximum ulna length versus maximum proximal width;* M. meri *Upp. Val.* = Mammuthus meridionalis *from Upper Valdarno;* E. ant *Fran.* = Palaeoloxodon antiquus *from Frankleben;* E. ant *Upp. Val.* = P. antiquus *from Upper Valdarno;* E. ant *Joz., Ciech., Grob., Grab.* = P. antiquus *from Jóźwin, Ciechanów, Gröbern and Grabschütz;* M. prim *Siberia, Mil.* = M. primignius *from Siberia and Milovice.*

in long bones. But the proportions, which would illustrate a more massive dorsal tubercle on the *arcus dorsalis* (atlas) and an extensive sculpture on the axis, have not been established here. These two vertebrae are morphologically similar, but metrically larger size in the male specimens.

## Discussion

The most reliable indicator of sex in the pelvis is the ratio of the aperture width and the acetabulum length. Lister (1996b) has reported that it is necessary to use a ratio for comparison because none of the pelvic measurements, taken alone, give a clear separation between the sexes: there is an overlap in the ranges of both sexes. However, skeletons are often found with this element missing and therefore cannot always provide sexing information from individual sites. On that account, the long bones, which preserve in larger quantities, are more preferable indicators of sexual differences, but only in large samples. The disadvantage of using long bones is that analysis can rely only on adult specimens, leaving out the remains of younger individuals.

The results of this investigation show a separation between males and females by using the measurements of long bones of adult specimens. Of course, this separation is based on individual species separately. In the samples available for study, the males slightly outnumber females in species *M. meridionalis* and *P. antiquus*. On the other hand, the species *M. primigenius* includes only adult females in the sample studied.

The deposits of Upper Valdarno and Frankleben were created by natural events, so this greater abundance of males could be the consequence of behavioral patterns. An analogy using the closest living species shows that elephants live in matriarchal family groups, where the young males are forced out at an age around 9–12 years, and the result is solitary individuals or small groups of young and adult males roaming the countryside and being at risk to dangers (Lister and Agenbroad 1994).

A different situation appears with *M. primigenius*, whose remains originate from sites where the bones were probably deposited by people (Svoboda 1991). Only adult females occur in these samples with a dominance of juvenile and subadult animals (personal observation). This observation of a higher frequency of younger animals than adults has been confirmed by several authors on the basis of teeth analysis from the same

site or the same type of site (Lipecki and Wojtal 1996; Pean: pers. comm.). Thus, the present study suggests as possible explanation that mammoths were selectively hunted according to their body size. Since body size varies by age and sex, the mammoths were selected by hunters according their age (preferred were the younger animals) and sex (preferred were the small females). Hunters apparently preferred to hunt mammoths occurring in groups, perhaps using strategies to isolate individuals for a more easy kill. Females and immature individuals would be less aggressive and thus less dangerous to hunt.

Were younger animals and adult females selectively hunted in comparison to adult males during this era? Although other explanations certainly exist, the human involvement appears the most probable reason. For confirmation of this hypothesis more materials are needed from human occupation sites, especially other measurements from localities of similar type and period.

*Acknowledgements*

I am very grateful to Elisabetta Cioppi, the curator of the Florence Museum of Geology and Palaeontology for her help and access to the collections. Thanks are due to Prof. Dietrich Mania for allowing me to examine the material mounted in Bilzingsleben. I am also indebted to Prof. Rudolf Musil, my supervisor, for his useful advice. I wish to thank Dr. Adrian Lister who offered useful comments and suggestions on an earlier draft of this paper.

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